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THE LAKE ATHABASCA SAND DUNES OF NORTHERN SASKATCHEWAN AND ALBERTA, CANADA

I. THE LAND AND VEGETATION

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Abstract

In northwestern Saskatchewan and in adjacent Alberta is a region of active sand dunes and desert-like topography that is unique botanically. Most of this region is underlain by Athabasca Sandstone from which the dune sand and gravel have been derived. During the recession of the Keewatin ice from the Mackenzie Basin, beginning 13 000–14 000 years ago the rivers flowing northward to the Arctic were impounded to form large proglacial lakes. By about 8500 years B.P. these lakes had been drained by the removal of ice from the Mackenzie valley to form glacial Lake McConnell. The shores of this lake have continued to be lowered, but much more slowly due to isostatic uplift in the eastern parts of the Athabasca and Great Slave Lake basins. It is proposed that these two lakes became separate bodies of water about 3300 years ago when the Fort Smith escarpment came to the surface. The sandy plain south of Lake Athabasca is believed to have been thus exposed rapidly at first, but more slowly in the last 8500± years.

The history and development of the sand dunes are closely linked to the lake shore processes that were effective during the past 9000-10 000 years. Strong winds were blowing over wide expanses of open water and over lands that were progressively exposed by the drainage of the lake and by isostatic rebound. Probably until 4000–5000 years ago the winds over most of the land were unobstructed by forests. The winds produced offshore bars and sandy beach ridges that were accentuated by ice push and transformed by the wind.

Habitats available for plant colonization in the region of actively blowing sand vary from dry sand, continuously blown about by the wind, to relatively stable soil surfaces. About 270 kinds of vascular plants, lichens, and mosses grow here. Aeolian sand appears in the form of sand dunes and sand sheets. The parabolic dune is the most common dune form in the region. The most conspicuous dunes in the active dune fields are the oblique ridge dunes that may reach heights of 35m above their bases. Large areas of rolling dunes and transverse dunes also occur in the active dune fields. Bordering the dune fields are precipitation ridges that invade forests, wetlands, rivers, and lakes. Gravel pavements appear as plains or ridges covered with a veneer of gravel often scoured and polished by wind and sand to form ventifacts. In dune slacks between active sand dunes the water table is sometimes exposed. Surrounding the open dune fields are extensive regions of stabilized aeolian topography covered by forest and wetland vegetation. Parabolic dunes often form in these areas following fire or other disturbance. These areas show their aeolian origins by the presence of stabilized dunes and ventifacts.

The vegetation of areas of active sand is made up of relatively few species but they occur in many combinations. Seedlings become established mainly in the moist to wet dune slacks, but a few species can establish themselves on the lee slopes of active dunes, on the dry gravel pavements, or on open sand plains. Vegetation within the active sand areas follows a cyclical pattern of establishment, burial, and re-exposure as the dunes move across the landscape. Seeds germinate and seedlings may become established in a moist dune slack. As a migrating dune invades the slack some plants are buried and killed and others remain above the sand surface by vegetative growth. In time, some of these plants appear on the lee slope and crest of the dune, but finally they are killed when they are excavated as the dune continues its migration. The gravel pavement habitat is relatively stable, but few species occupy it. Only about 10 species of vascular plants occur here, some of which are taproted perennials with arctic affinities.

On stabilized sand areas the most common forest type is open *Pinus banksiana*-lichen forest. Over 60 species occur in this habitat but the floristic composition at any one place may be very simple, sometimes consisting of only one or two vascular plant species. Mesophytic forests on floodplains and ridges are floristically variable, and the primary species may be various combinations of *Pinus banksiana*, *Picea mariana*, *P. glauca*, and *Betula papyrifera*. Wetlands are common and appear in the form of muskeg forested with *Picea mariana* and *Larix laricina*, muskeg shrub vegetation, and grass-sedge meadows.

Résumé

Dans le nord-ouest de la Saskatchewan et la partie adjacente de l'Alberta se trouve une région aux dunes vives et aux reliefs semi-désertiques qui, au point de vue de la botanique, ne ressemble à aucune autre. La plus grande partie de cette région repose sur une couche de grès de l'Athabasca, dont sont issus le sable et le gravier des dunes. Au cours du retrait des glaces du Keewatin, qui ont commencé à se retirer du bassin du Mackenzie il y a 13 ou 14 000 ans, les rivières qui coulaient vers le nord jusqu'à l'Arctique se trouvèrent endiguées, donnant naissance à de grands lacs. Dès 8 500 ans avant le présent, ces lacs avaient été drainés par le retrait des glaces obstruant la vallée du Mackenzie, et avaient formé le lac glaciaire McConnell, dont les rives s'abaissent encore, mais beaucoup plus lentement à cause du soulèvement isostatique des parties orientales des bassins de l'Athabasca et du Grand Lac des Esclaves. On a avancé l'hypothèse que ces deux lacs sont devenus des nappes distinctes il y a environ 3 300 ans, lorsqu'affleura l'escarpement de Fort Smith; la plaine sablonneuse située au sud du lac Athabasca aurait été ainsi mise à découvert d'abord rapidement, puis plus lentement au cours des dernières 8 500 années, plus ou moins.

L'histoire et le développement des dunes sont étroitement liés à la transformation des rives depuis 9 à 10 000 ans. Des vents violents soufflaient sur de vastes étendues d'eaux libres et sur des terres qui émergeaient peu à peu par suite du drainage des lacs et du relèvement isostatique. C'est probablement il y a 4 ou 5 000 ans que des forêts commencèrent à faire obstacle aux vents qui jusqu'alors balayaient presque toutes les terres. Ces vents produisirent des cordons littoraux et des crêtes de plage sablonneuses, accentués par la pression des glaces et transformés par le vent.

Dans cette région où le sable se meut continuellement, les habitats susceptibles d'accueillir la vie végétale varient, la gamme allant de ceux qui sont recouverts de sable sec, constamment véhiculé par le vent, à ceux où les sols ont des surfaces relativement stables. Environ 270 espèces de plantes vasculaires, de lichens et de mousses y croissent. Le sable éolisé se présente sous forme de dunes et de nappes, la dune parabolique étant la dune dont le type est le plus répandu dans la région. Dans les champs de dunes vives, les dunes les plus remarquables sont les dunes aux crêtes obliques dont la hauteur s'élève parfois jusqu'à 35 mètres à partir de la base. Les champs comptent aussi bon nombre de dunes onduleuses et transversales. En bordure des champs de dunes, des crêtes envahissent par vagues successives les forêts, les marécages, les rivières et les lacs. Des sols de gravier apparaissent sous forme de plaines ou de crêtes recouvertes d'une pellicule de gravier aux éléments souvent décapés et polis par le vent et le sable pour former des cailloux éolisés. Dans les creux qui séparent les dunes vives, la nappe phréatique affleure parfois. Les champs de dunes sont entourés de vastes régions à la topographie éolienne stabilisée, couvertes de forêts et de végétation marécageuse. Des dunes paraboliques s'y forment souvent à la suite d'un incendie ou d'une autre perturbation. L'intervention du vent se manifeste par la présence de dunes stabilisées et de cailloux éolisés.

La végétation des zones de sable actif est constituée d'un nombre relativement restreint d'espèces aux combinaisons toutefois multiples. Les jeunes plantes s'établissent principalement dans les creux moites ou humides, mais quelques espèces peuvent se fixer aux pentes sous le vent des dunes vives, sur les sols de gravier sec ou dans les plaines de sable libre. Dans les zones de sable actif, la végétation suit un cycle : établissement, enfouissement et réapparition à mesure que les dunes se déplacent à travers le paysage. Des graines germent et de jeunes plantes peuvent apparaître dans un creux humide. Lorsqu'une dune en migration envahit le creux, certaines plantes sont ensevelies et tuées tandis que d'autres restent au-dessus de la surface du sable à cause de leur croissance végétative. Avec le temps, certaines d'entre elles apparaissent sur la pente sous le vent et la crête de la dune, mais elles sont finalement déracinées et périssent lorsque la dune poursuit sa migration. Le sol de gravier constitue un habitat relativement stable, mais rares sont les espèces qui l'occupent. N'y poussent qu'environ 10 espèces vasculaires, dont certaines plantes vivaces à racine pivotante proches de la végétation arctique.

Dans les zones de sable stabilité, le type forestier le plus répandu est celui de la forêt claire à dominante de *Pinus banksians* et de lichens. Plus de 60 espèces vivent dans cet habitat, mais la composition floristique à un endroit quelconque

peut être très simple et consister parfois en une ou deux espèces de plantes vasculaires. Les forêts mésophytiques des plaines inondables et des crêtes ont une flore qui varie, les principales espèces pouvant être diverses combinaisons de *Pinus banksiana*, *Picea mariana*, *P. glauca* et *Betula papyrifera*. Les terres humides sont communes et se présentent sous forme de muskegs aux forêts de *Picea mariana* et de *Larix laricina*, de muskegs à végétation arbustive ou de prairies d'herbes et de carex.

Introduction

On the south shore of Lake Athabasca in northwestern Saskatchewan lies a great sand "desert," a wilderness area of shifting sand, high sand dunes, and gravel pavements covered with wind sculptured and polished stones. The active dunes are invading and overwhelming the surrounding forests which are unable to stabilize the moving sand. The very sparse vegetation of the active sand is made up of a unique assemblage of plants derived from arctic, boreal, and Great Plains elements. Some of these are disjunct from their parent populations, and others are endemics which occur only in the sand dune region.

The desert-like areas of loose sand lie bordering on or within about 1.5 km of the lake shore and most of them subtend that portion of the shore between Ennuyeuse Creek and the MacFarlane River. To the west, in northeastern Alberta, there is a small area of open sand west of the Maybelle River and another west of the Richardson River. The sand dune fields range in altitude from about 214 m, a meter or two above the elevation of Lake Athabasca, to about 335 m above sea level. The largest areas of active aeolian sand are located where the William and the MacFarlane Rivers meet the lake. Between these points, and parallelling the lake shore, are a number of smaller open dune areas (Figure 1 and Appendix A).

The active dune system consists of complexes of sand dunes ranging from ridges up to 35 m high unstabilized by vegetation to low dunes thinly covered by grasses and shrubs. In places sand dunes are moving across partially stabilized gravel pavements and exposed water tables or they form unstable sheets of loose sand. Except in a few places where sand comes out to the lake shore, the areas of active sand are surrounded by more stabilized sand plains, dunes, or elongated sandy-gravel ridges.

The Lake Athabasca sand dunes were known in prehistoric times to travellers who left behind stone tools and projectile points that mark their

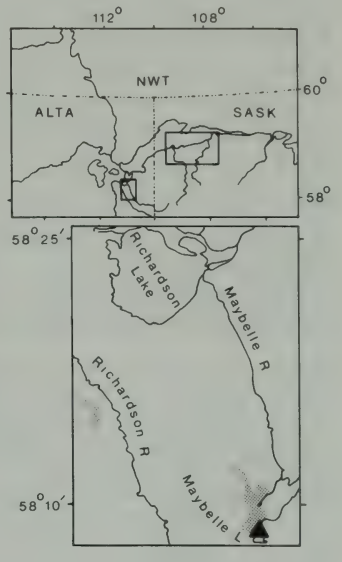
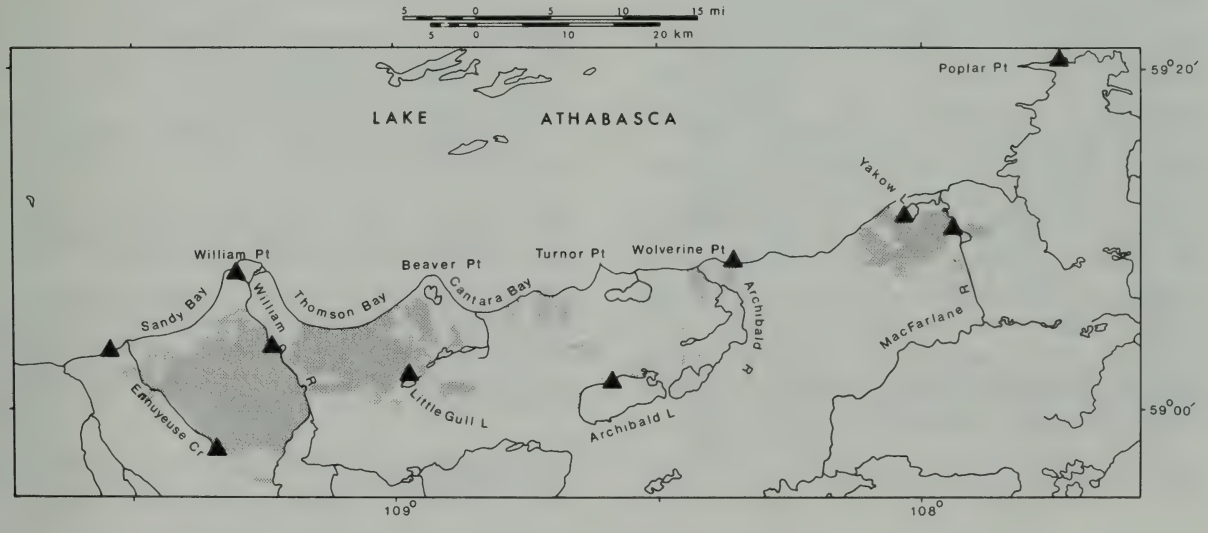


Figure 1

Map of the active sand dune region south of Lake Athabasca. The active dunes are shown as stippled areas. The field camps of our parties are shown as triangles.



presence (Wright, 1975). Small "workshops" in the form of boulders surrounded by flakes produced in the fabrication of stone tools have been found in some of the boulder deposits associated with gravel pavements. The earliest written record of the existence of the sand dunes was made in 1791 by Philip Turnor who wrote that as he approached the delta of the William River he could, "see about 3 miles East and round to SSW all a rising sandy desert of a yellowish white Colour with a chance scub pine standing singly" (Tyrrell, 1934, p. 427). As he passed the MacFarlane River he saw, "heigh sandy hills which when seen off the mouth of the river looks like fields of ripe corn between ledges of woods such as are seen in the Hill countrys of England" (Tyrrell, 1934, p. 429).

Turnor's was not only the first mention of this great sand dune area but the only one for 100 years until the geologist D.B. Dowling travelled up the William River in 1892 and noted, "on the surface of the plateau, which is mostly bare, sand-hills rise in some cases nearly a hundred feet above the general level" (Tyrrell & Dowling, 1897, p. 70D). These brief observations were not developed further by Dowling, who gave the name "Athabasca Sandstone" to the horizontally bedded Precambrian formation underlying the terrain. Inexplicably, the early explorers who visited the south shore of Lake Athabasca did not seem to recognize the uniqueness of the great sand "desert" that lay to the south. It was not until the 1920's and 1930's, when aerial photographs became available, that there was a full realization of the distribution and extent of the active sand dune areas. But there are other reasons for the silence about the sand dunes over so many years.

On a stormy day the pinkish reflection of the wet sand on the low lying clouds may serve as a beacon to travellers, but the south shore of Lake Athabasca is not hospitable. The lakeshore from Ennuyeuse Creek to the MacFarlane River is characterized by wide sand beaches and sandy shoals. Travel by canoes or other small boats is hazardous because northwesterly and northeasterly winds are frequent and often violent, making it imperative to get boats and their contents ashore quickly. Safe anchorages are nonexistent. The result has been routine avoidance of the south shore by nearly all travellers on the lake; only two or three trapper's cabins are to be found there.

To the casual visitor the aeolian sand areas appear to be covered very sparsely by plants and to resemble sand dunes of the maritime coasts of North America. The botany of the sand dunes was first studied by H.M. Laing who accompanied the naturalist Francis Harper to Lake Athabasca in 1920. His plant collections are in the United States National Herbarium, but no report is known to have been written. The next botanical collections were made in 1935 by Hugh M. and Lucy G. Raup. The flora of the sand dunes proved to be interesting in that it consists of species that have been derived from the waves of arctic, boreal, and northern Great Plains floras that moved into the region following deglaciation and climatic amelioration. Among plants that were isolated in the active sand dunes are some that are morphologically distinct from their parental populations and have been recognized as endemic taxa (Raup, 1936). This in itself is remarkable because the Mackenzie Basin is not noted for its endemism, and the discovery of a pocket of endemics in a vast region otherwise devoid of them presents intriguing problems in the evolutionary and geographic history of the flora.

Comparable areas of inland sand dunes in North America are few. The Lake Michigan sand dunes, described by Cowles in 1899 and later studied in detail by Olson (1958), and the Kobuk River sand dunes in Alaska (Fernald, 1964; Ricciuti, 1979) are the only similar areas of active sand dunes known to us. These areas, however, are much smaller in extend than the Lake Athabasca dunes and have different floras. The Lake Michigan flora has many deciduous forest taxa unknown in boreal Saskatchewan, but there are some species in common, as well as numerous species that occupy a similar niche and are in a sense vicariads. The floras of the Kobuk River dunes and the Lake Athabasca dunes, while different, have a number of species in common. The landscape of the Great Kobuk dunes is also similar in having active dunes up to 35 m high.

Endemism in the Lake Michigan and Kobuk River dunes is much less than at Lake Athabasca. *Oxytropis kobukensis* Barneby is endemic to the Kobuk dunes and a sand dune ecotype of *Astragalus alpinus* L. has been collected there (C.H. Racine, pers. comm.); but other taxa such as *Deschampsia caespitosa* (L.) Beauv., *Salix alaxensis* (Anderss.) Cov., *Silene acaulis*[1], *Armeria maritima*, and *Tanacetum huronense* that have

[1]Authorities for taxa in the flora of the sand dune region are given in Appendix B.

differentiated in the Lake Athabasca region, into *Deschampsia mackenzieana*, *Salix silicicola*, *Silene acaulis* f. *athabascensis*, *Armeria maritima* ssp. *interior* and *Tanacetum huronense* var. *floccosum* respectively, have apparently not undergone similar changes in the Kobuk River region. In the Lake Michigan sand dunes the only endemic appears to be *Salix syrticola*. Fern. (usually included in *S. cordata* Michx.) a willow that has the thickened and densely villous leaves similar to some of the Lake Athabasca *Salix*.

In this paper we will describe the aeolian sand areas and their vegetation and place the area into a broad geographic context. In order to rationalize the existence of endemic plants in the active sand dunes we will present a geographic study of aeolian sand habitats as they existed or probably existed throughout postglacial time in northern Alberta and Saskatchewan and in the continental Northwest Territories. This will involve a review of events following the recession of glacial ice, the resultant landforms and soils, climatic changes during the period, the development of vegetation and the migration of native people and game animals into the region. We know that all these events happened in the 13 000–14 000 years since the glacial ice began to recede eastward from its western maximum extent, but, although some of the major events left clear marks in the landscape, the details remain hazy and speculative.

Our study of the Lake Athabasca sand dunes is presented in two parts. In the first part the landscape—its physiography and vegetation and some phytogeographic relationships is described. The second part, to appear later, will catalogue the flora and will consider its geography and the nature and origin of botanical endemism in the Lake Athabasca region.

We make no pretense to the completeness of this work. At best it can be regarded as a reconnaissance set down here in the hope that it will stimulate further and more sophisticated study.

Materials for the Present Paper

Collections from the dune areas were made in 1935 by Hugh M. and Lucy G. Raup. They spent the last week of July and all of August on the south shore of the lake working from four base camps (Figure 1).

1. *Ennuyeuse Creek*, 3 km west of its mouth: Lat. 59°03′, Long. 109°34′
2. *William River*, 1.5 km above its mouth: Lat. 59°08′, Long. 109°19′.
3. *Wolverine Point*, 3 km east of the point: Lat. 59°09′, Long. 108°25′.
4. *Poplar Point*, 8 km east of the point: Lat. 59°30′, Long. 107°41′.

Brief stops for collecting and reconnaissance were made at several other places. The vascular plant collections of 1935 were reported by Raup (1936) as were his notes on the forests south of the lake (Raup, 1946). Several endemic taxa found growing on the dunes were described and named in the 1936 paper, but numerous notes on the dunes and their vegetation have remained unpublished. Data on shoreline and muskeg vegetations in the dune areas, however, were used in a paper on species versatility in shoreline habitats (Raup, 1975).

Later field work on the dune areas was done by George W. Argus in four visits between 1962 and 1975. These trips were accomplished by air travel, which enabled him to approach the dunes from the south and to establish base camps on small lakes at or near the southern borders of the large dune areas where no studies had previously been made (Figure 1). During each visit both vascular and non-vascular plants were collected and notes made on the dunes and their vegetation. In 1963 and 1972 living material was obtained for cultivation.

1. *Maybelle River*, lake at the head of the river: Lat. 58°09′, Long. 110°53′. 30 July – 2 August 1975, with David J. White, assistant.
2. *Ennuyeuse Creek*, small lake at the head of the creek: Lat. 58°58′, Long. 109°20′. 10–15 August 1975, with David J. White.
3. *William River*, west side of the river 10 km from its mouth: Lat. 59°03′, Long. 109°11′. 26–28 July 1972, with Thomas Kovacs, Parks Canada.
4. *Little Gull Lake*: Lat. 59°02′, Long. 108°59′. 26 June–10 July 1962, with Robert W. Nero, ornithologist, George F. Ledingham, naturalist and F.H. Edmunds, geologist; 31 July–3 August 1963, with Robert W. Nero; 3–9 August 1975, with David J. White.
5. *Archibald Lake*: Lat. 59°09′, Long. 108°36′. 29–30 July 1972.
6. *Yakow Lake*, at the edge of the dunes: Lat. 59°12′, Long. 108°02′. 17–23 July 1962, with Robert W. Nero.

7. *MacFarlane River*, at the edge of the dunes 4 km above the mouth of the river: Lat. 59°11′, Long. 107°55′, with Thomas Kovacs.

Other recent research in the dune area was done in 1971 when Reinhard Hermesh, then a graduate student at the University of Saskatchewan, made a short reconnaissance visit to the sand dunes in May and then spent June, July, and August in a more detailed study. His unpublished thesis (Hermesh, 1972) contains a major contribution on the plant ecology of the dunes and will be referred to repeatedly in the present paper. He worked from the lake shore, from a camp at Ennuyeuse Creek, and from Thomson Bay. He visited the MacFarlane River dunes only briefly toward the end of the season. He investigated dune forms, especially their relations to winds and local water tables, and attempted a classification of them. Especially valuable are his studies involving excavation and illustration of the growth habits of dune plants.

In the summer of 1977 Dr. Derald G. Smith, engaged in a long-term study of sand bars and channel braiding processes in the William River delta, prepared a reconnaissance report on dunes of the large fields on either side of the William River (Smith, 1978). He classified the dune forms and discussed the Athabasca Lake beaches and the formation of beach ridges.

Between 1971 and 1976 Maureen Landals studied the sand dune area between the Maybelle and Richardson Rivers in northeastern Alberta. The main objective of her study (Landals, 1978) was to assess this region as a potential park. In the course of her work she studied the dune forms, their origin, and their vegetation.

Dr. Peter P. David included the Lake Athabasca dune area in his general description of the sand dune topography of Canada. In his report (David, 1977) he assigned new names to the areas of aeolian topography in our region. The Maybelle River dunes described in our paper are in his "Richardson River Sand Hills," while all the others immediately south of Lake Athabasca, which we discuss in detail, are in his "Archibald Lake Sand Hills." We prefer to retain the name "Lake Athabasca sand dunes" for our region not only because of its long usage (Raup, 1936; Hermesh, 1972; Rowe & Hermesh, 1974; Smith, 1978) but also because the postglacial history of the area is closely related to the development of Lake Athabasca itself.

Geology and Physiography

General Geology

A major geological boundary traverses central Saskatchewan, northeastern Alberta, and the District of Mackenzie to Great Bear Lake and the arctic coast. East and northeast of this boundary is the Canadian Shield underlain by hard Precambrian rocks: granite, gneiss, sandstone and quartzite, highly metamorphosed Archean sedimentary rocks, and volcanics. West of the boundary are mainly softer sedimentary rocks of Paleozoic or, at higher levels, Cretaceous age. This difference is reflected dramatically in the glacial drift deposits and the soils derived from them.

Of particular significance to the present paper are the areas directly underlain by the Precambrian sandstones, for they are the ultimate source of the Athabasca dune sands as well as of most of the aeolian sands of the region. The major areas of sandstone were mapped by Fahrig (1961) and are shown here as Figure 2 (with modification). Probably the most extensive is the Athabasca Sandstone (Tyrrell & Dowling, 1897; Alcock, 1936; Blake, 1956; Fahrig, 1961) which underlies most of Lake Athabasca, appearing on islands in the lake and cropping out in a few places on the north shore. Eastward its border extends to Black and Wollaston Lakes, southward and southeastward to Cree Lake and the Mujatik River. It is bordered on the south and west by the Precambrian Shield margin, reaching Lake Athabasca west of Old Fort River.

Deglaciation

The Keewatin ice sheet covered a vast region from Hudson Bay westward nearly or actually to the base of the Rocky and Mackenzie Mountains. There it met with Cordilleran ice or left in some places a corridor between. It appears to have started melting back about 13 000 to 14 000 years ago (St-Onge, 1972; Ritchie & Hare, 1971; Craig & Fyles, 1960; Prest, 1969). Craig & Fyles (1960, p. 10) have proposed that "The last remnants of the Laurentide ice-sheet west of Hudson Bay could not have survived much later than 7,000 years ago and may have disappeared earlier."

Postglacial Lakes

With the recession of the ice, waters of the great rivers draining to the Arctic were impounded by

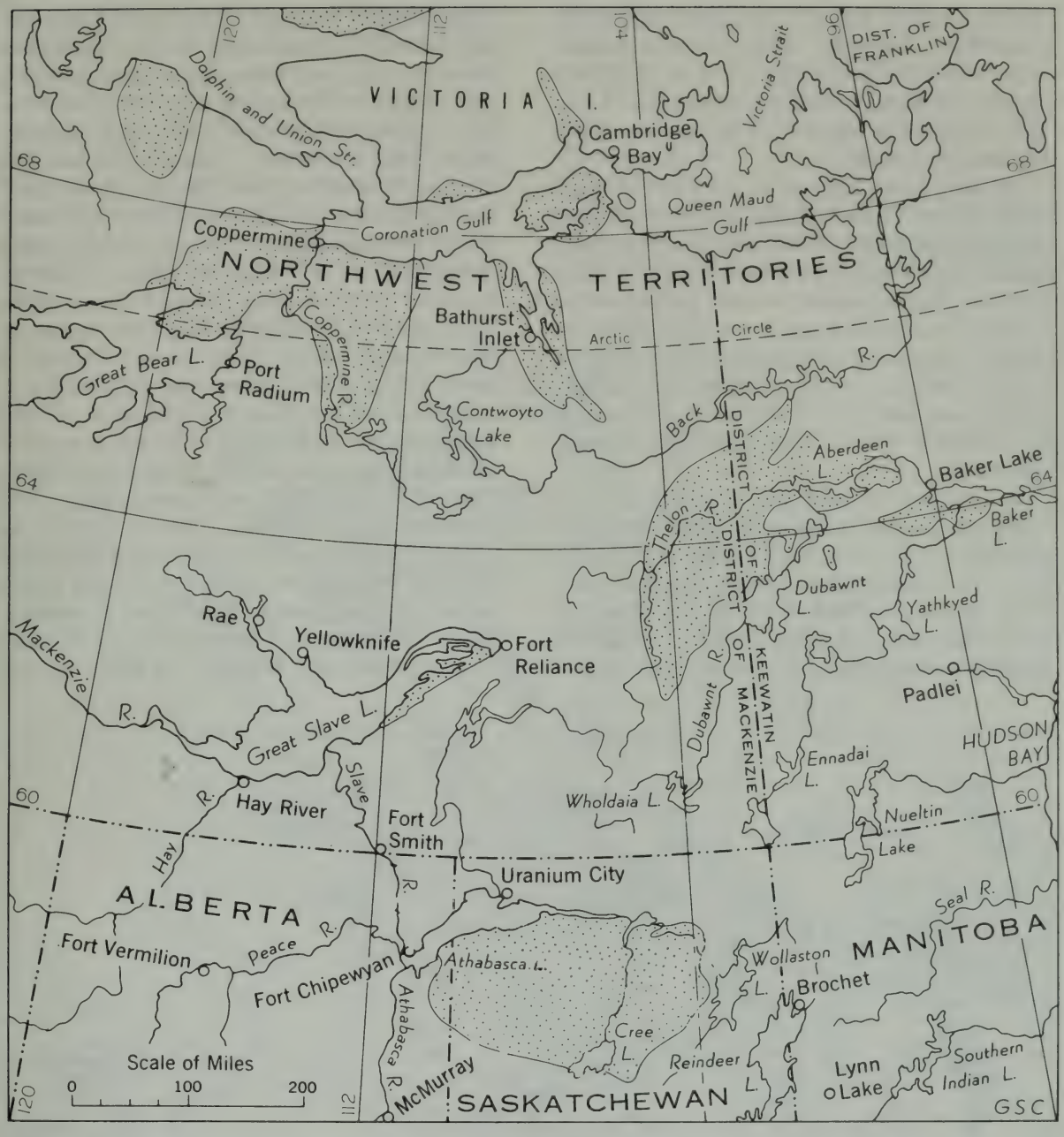


Figure 2. Areas (stippled) underlain by sandstone bedrock in northwestern Canada Modified from Fahrig, 1961 (used with permission).

the ice front to form a series of great lakes at progressively lower levels. These lakes covered wide areas in the depressions that now carry the major rivers and the great northern lakes. As the ice melted back across the Canadian Shield it formed smaller lakes of shorter duration in the drainage basins of such rivers as the Dubawnt, Thelon, and Back (see Craig & Fyles, 1960; Taylor, 1956). The glacial ice produced another effect which is of great significance in the history of these postglacial landscapes. It depressed the earth's crust under its weight and, as the ice withdrew, upward readjustments took place. Firm data on this effect are inadequate for more than rough estimates of its magnitude and distribution.

The earliest of the postglacial lakes in central Alberta mapped by Taylor (1960) is called "Miette Lake." It was a narrow body of water, about 160

km (100 mi) long and at an altitude of about 952 m (3450 ft) in the upper valley of the Athabasca River where the latter flows out from the Rocky Mountains through the foothills. It flowed into Lake Edmonton which flowed into the North Saskatchewan River.

Another great lake system was in the Peace River basin. Taylor (1960) indicated that the uppermost deposits of this lake, which has been called "Lake Peace," are at an altitude of 984 m (3225 ft). As the lake was lowered by the receding ice front, lacustrine deposits were laid down at a series of successive levels from west to east down to about 444 m (1750 ft) at which point the lake became confluent with the highest level of a large body of water which Taylor called "Lake Tyrrell" (Figure 3).

A long arm of Lake Tyrrell extended up the valley of the Peace River to the above altitude of about 444 m (1750 ft). Taylor (1960, p. 175) cited the work of Lindsay *et al.* (1958b, map sheet 84-F; 1960, map sheets 84-J & 84-K) who, "mapped three large areas of sandy aeolian and alluvial materials adjacent to the modern Peace River." These deposits were 590, 1170, and 1271 km^2 (228, 452, and 491 square miles) in area, with their upstream ends at elevations of approximately 427, 336, and 275 m (1400, 1100, and 900 ft) above sea level, respectively. Taylor (1960, p. 175) interpreted these as, "deltas . . . , whose materials have been partly reworked into dunes by wind action." He regarded these deltas as evidence of still-stands in the drainage of Lake Tyrrell. Probably they correspond to the stages estimated earlier by Cameron (1922) at 488, 335, and 244 m (1600, 1100, and 800 ft). Another long arm reached up the Athabasca River valley to an elevation of about 549 m (1800 ft) above sea level. This is at approximately the lower end of a series of sand dunes mapped by St-Onge (1972) and is at about the same place in the valley that marks the highest level of Lake Tyrrell on Taylor's map. This elevation is very near the lowest level given by Taylor for the confluent Lake Peace (534 m or 1750 ft). He extended Lake Tyrrell only provisionally into the present basin of Lake Athabasca. At the highest level of Lake Tyrrell, presumably attained while the Mackenzie Valley was still

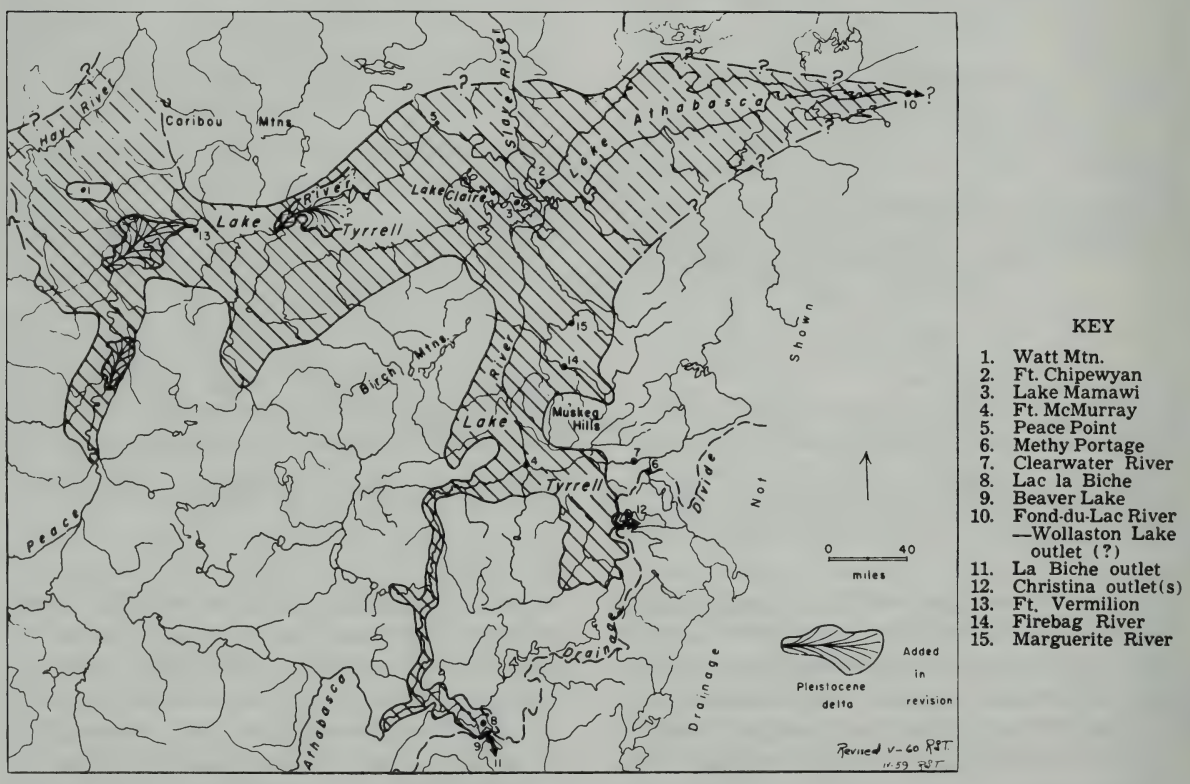


Figure 3. Approximate limits of glacial Lake Tyrrell. Lake Peace extends up the Peace River valley. From Taylor, 1960 (used with permission).

obstructed by ice, its drainage probably was southeastward into the Churchill River basin (Taylor, 1960).

Craig (1965) drew provisional boundaries of an ancestral Great Slave Lake, which he called "Lake McConnell" (Figure 4). From the locations and altitudes of old shorelines, deltas, and other features, Craig thought that this lake reached its greatest extent at approximately the present altitude of 282 m (925 ft) above sea level. This altitude for the highest known shores was found near Faber Lake, which is 80 km (50 mi) north northwest of the end of the North Arm of Great Slave Lake, and also near the northeast shore of Buffalo Lake. At this time the glacial margin was about at the western edge of the Canadian Shield, and the western extremity of the lake was in the upper Mackenzie valley, down at least to the Liard River (Craig, 1965). Using the elevations of deltas near Fort Simpson (153 m or 500 ft) and the one near

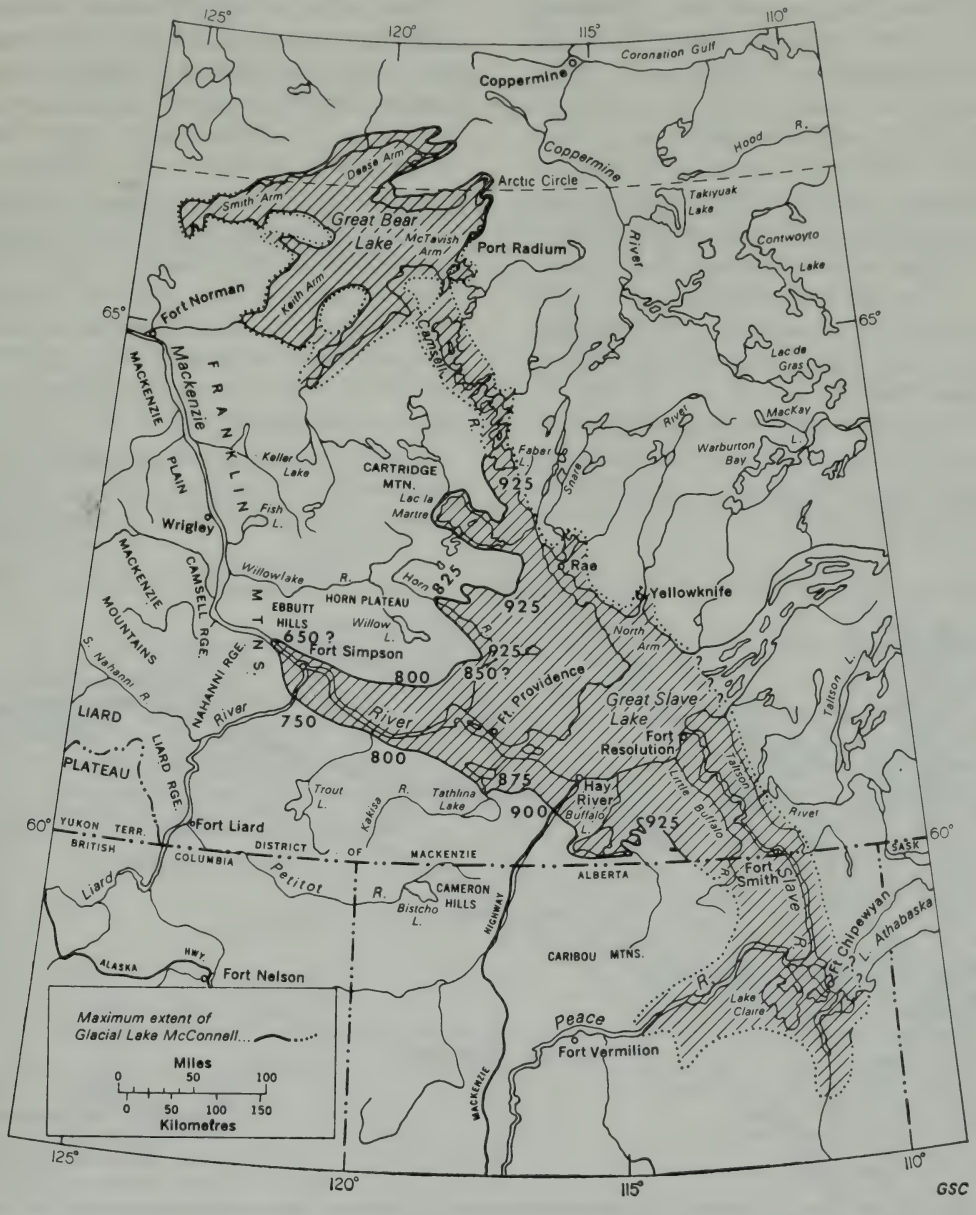


Figure 4. Glacial Lake McConnell. The approximate elevations (in feet) around the western extent of glacial lake McConnell are from Craig, 1965, Fig. 2. Modified from Craig, 1965 (used with permission).

Faber Lake (282 m or 925 ft), he estimated that the differential isostatic rebound in this area was a little over 38 cm per km (2 ft per mi). He proposed that the lowest delta mapped by Taylor in the Peace valley probably formed at the shore of Lake McConnell. He thought that Great Slave and Great Bear Lakes probably were also connected at this time. He did not have enough data to propose a position for the ice front in the Athabasca Lake basin; but he was convinced that when Lake McConnell was formed the Mackenzie drainage had already been restored and that subsequent drainage of the lake was caused by uplift in the eastern part of the basin.

From the above notes, it appears that Lakes McConnell and Tyrrell overlapped in a strait perhaps 80 km (50 mi) wide over the Slave River valley. The lakes continued to be joined until the combined lake fell to about 206 m (675 ft) above sea level. At this level the bedrock escarpment, which now forms the Smith Rapids in the Slave River, was exposed at the surface. It formed a dam that held up Lake Athabasca while Great Slave Lake continued to fall.

For convenience in the following discussion, only that part of the combined lake that was above the uppermost shores of Lake McConnell will be considered as Lake Tyrrell.

An eastward extension of Lake McConnell that covered all or most of the basin of the present Lake Athabasca now seems probable. Cameron (1922) thought that at his 335 m (1100 ft) level the lake covered approximately the western half of the basin, and that at his 244 m (800 ft) level all of the basin would be covered. Prest (1969) estimated that the Athabasca Lake basin was clear of ice by about 9000 years ago. If this estimate is correct, Lake McConnell probably had a long arm extending into the Athabasca Lake basin.

Because the ancient dimensions and shore configurations of Lake Athabasca are of great significance in the development of the dune country and its vegetation, we venture a tentative reconstruction of the Lake McConnell shore lines. Our reconstruction is based on a projection of an isostatic rebound rate of 38 cm per km (2 ft per mi) to the east approximately at right angles to the presumed ice margin. East of Old Fort Point the shore would have been near the present 305 m (1000 ft) contour, south of William Point it may have been near the present 335 m (1100 ft) level, and at the MacFarlane River near the present 366 m (1200 ft) level (Figure 5).

Beaches as high as those projected for Lake McConnell have not been found in the Lake Athabasca basin. However, Taylor (1960, p. 173)

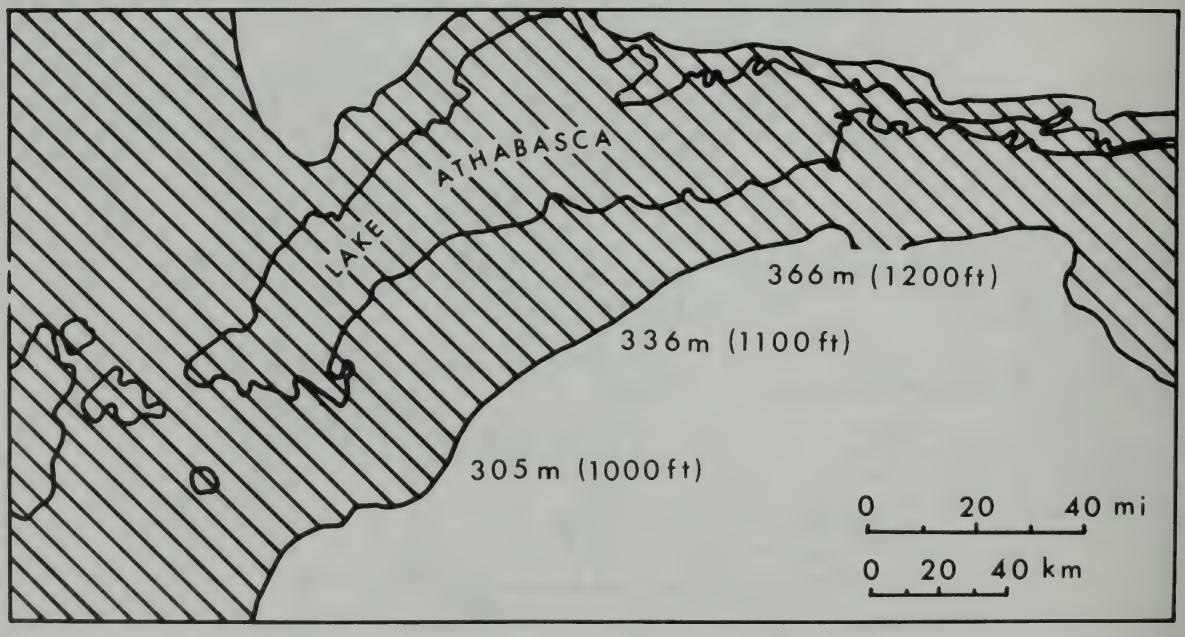


Figure 5. Suggested projection of Lake McConnell (Figure 4) into the Lake Athabasca basin when its elevation at Buffalo and Faber Lakes was approximately at the present 282 m (925 ft) contour. Elevations indicate the approximate present levels.

stated "Many shorelines occur on the Shield rocks north of Lake Athabasca, but even the highest of these appears to be no more than 1000–1050 feet above sea level." These elevations came from the country around the north angle of the lake, and they approximate the elevation we have proposed for the southern shore of Lake McConnel south of William Point (ca. 330 m or 1100 ft contour). Our projection of Lake McConnell into the Athabasca Lake basin carries the assumption that higher raised beaches will eventually be found above the eastern shores of the lake.

As the glacier receded eastward toward the Keewatin Ice Divide (Lee *et al.*, 1957) the northeastward drainage of rivers such as the Thelon, Dubawnt, and Kazan was impounded to form lakes. The geography of these lakes, in both space and time, has had no more than reconnaissance study. Craig & Fyles (1960) summarized knowledge of them as follows:

In the western part of Thelon River basin, beaches have been found up to about 381 m (1250 ft). They become progressively lower eastward to about 214 m (700 ft) at Beverly Lake. A proglacial lake in the Dubawnt basin left beaches up to about 275 m (900 ft) on the east side of the present lake. In the Ennadai Lake – Kasba Lake basin the highest beaches have been found at about 384 m (1260 ft) above sea level.

Table 1. - Estimated Time Periods for Deglaciation, Postglacial Lakes, the Xerothermic Period, the Advance of Forests, and the Occurrence of Aeolian Sand Activity in Northwestern Canada.

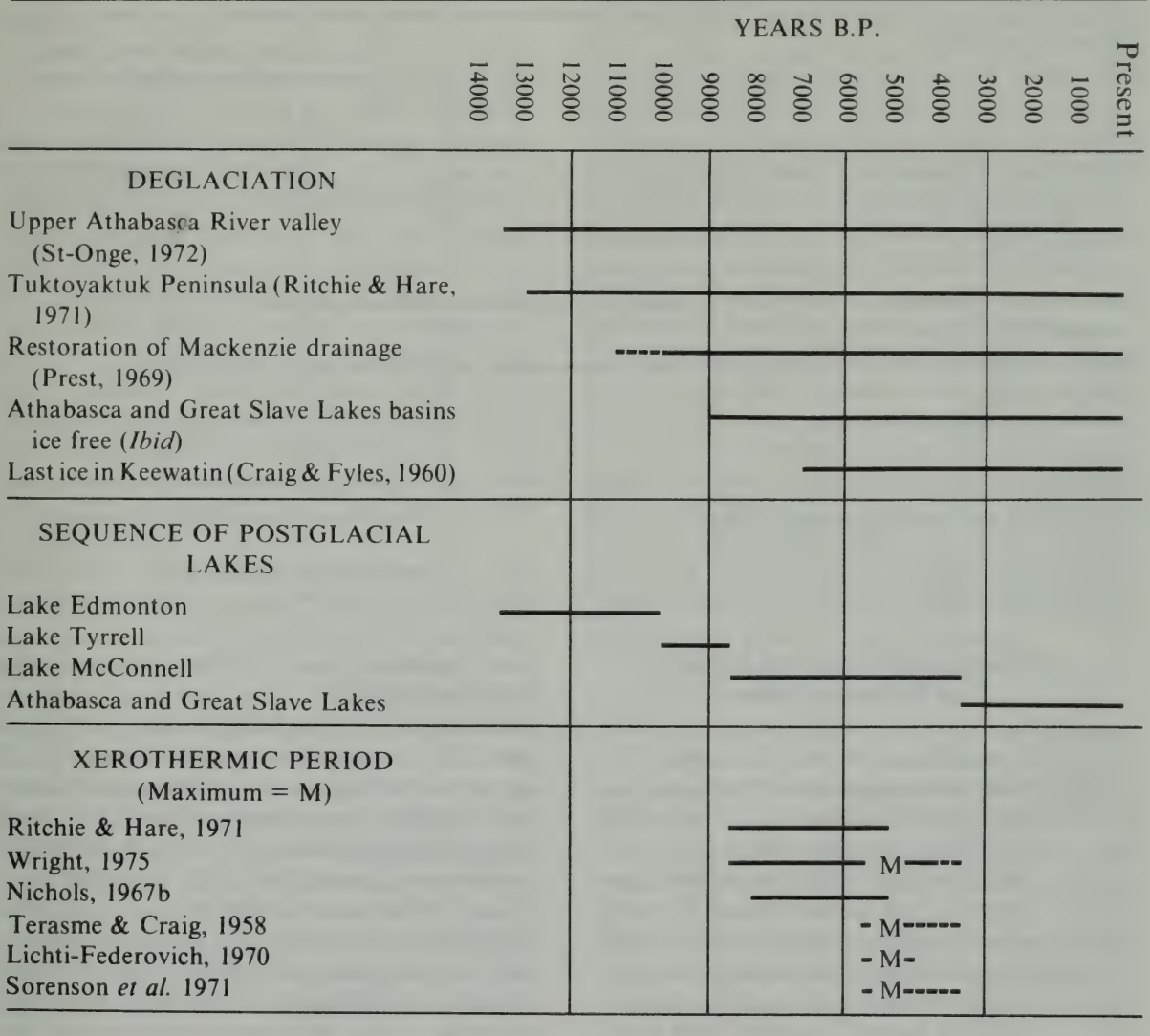
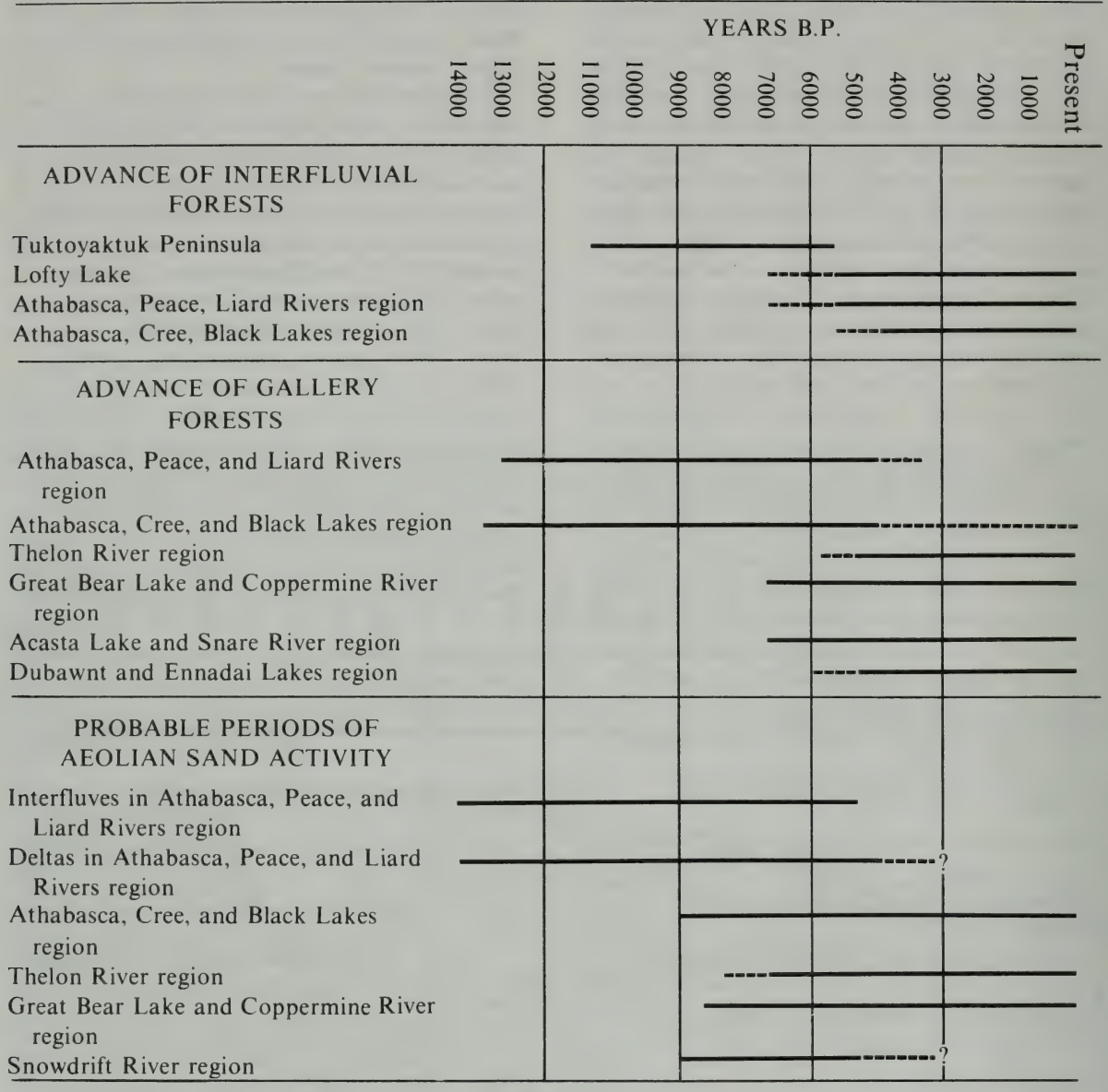


Table 1. (Cont'd) - Estimated Time Periods for Deglaciation, Postglacial Lakes, the Xerothermic Period, the Advance of Forests, and the Occurrence of Aeolian Sand Activity in Northwestern Canada.



Deglaciation and Tentative Dating of the Postglacial Lakes

Dates for the formation and drainage of the postglacial lakes remain speculative and can give, at best, only a general outline for the timing of these events (Table 1). This outline suggests, however, probable limits for some of the time periods with which we are concerned. Rates of drainage are uncertain because the ice margin was stationary for sometime in the lakes above Lake McConnell, and because inadequate values for isostatic uplift are known. Isostatic uplift is affected by crustal hinge lines that have not been located and studied.

St–Onge (1972, pp. 12-14) gave a date of 13 500 years B.P. for samples taken from above the till left by the melting glacier. These samples came from the uppermost dune area that he described along the upper Athabasca River. At about 50 km downstream from this point he reported dates around 10 000 years B.P. We have no analogous early dates for the retreat of ice from the mountain fronts in the upper Peace and Liard River valleys.

Mackay & Mathews (1973) dated floodplain sediments in the Mackenzie valley above the

Ramparts at 11 000–11 500 years B.P., indicating that at least the lower part of the valley was open at this time. Ritchie & Hare (1971) have given a date of 12 900 years B.P. for the first tundra vegetation on the Tuktoyaktuk Peninsula just east of the Mackenzie River delta. Craig & Fyles (1960) concluded from ^{14}C dates available at that time, that the Laurentide ice sheet west of Hudson Bay could not have survived much later than 7000 years ago and may have disappeared earlier.

If the first appearance of tundra vegetation marks approximately the beginning of ice retreat in the west, the ice front retreated through a distance of roughly 1450 km in about 6000 years. At this rate it may have reached the western margin of the Canadian Shield by about 10 000 years B.P. and may have cleared the Athabasca and Great Slave Lake basins by about 9000 years B.P. This agrees with Prest's estimate (1969) of 9000 years B.P. for the clearance of Lake Athabasca.

These dates suggest a time sequence for the drainage of Lake Tyrrell down, at least, to the level of the uppermost beaches of Lake McConnell described by Craig (1965). Assuming that Lake Tyrrell, and some phase of Lake Edmonton were essentially confluent in the upper Athabasca River valley, and using St-Onge's date from near the lower end of his dune area (St-Onge, 1972), a tentative date for the beginning of Lake Tyrrell is about 10 000 years B.P. Using Prest's estimate of 10 000–11 000 years B.P. for the opening of the upper Mackenzie River valley, Lake Tyrrell would have been rapidly drained down to the level of the uppermost beaches of Lake McConnell. Below this level its drainage would have been much slower as "timed" by the rate of isostatic rebound (Craig, 1965).

The rise of the land surface with respect to the lake levels appears to have been relatively slow and fairly steady during the last few thousand years. Cameron (1922), working at Windy Point on Great Slave Lake, counted 100 beaches over about 76 m (250 ft) of altitude to the crest of a hill where a horsehoe beach was formed as the land rose above the lake. He described the beaches as, "fairly uniform in depth, and throughout most of the rise occur as a series of very regular waves...." (Cameron, 1922, p. 353). His description could be applied, almost without change, to the raised beaches measured by our field party in 1935 at Charlot Point, Lake Athabasca, even to the horseshoe beach at the top of the hill. Here the beaches extend up to about 73 m (240 ft) above the lake in a horizontal distance of about 3.8 km (2.4 mi), and on a slope of about 6°.

Higher raised beaches are found around the eastern end of Great Slave Lake, up to 165 m (540 ft) above the present lake level (Stockwell, 1933). Blanchet (1926a), who described the Lockhart River valley up to 13 km (8 mi) above its mouth at Great Slave Lake, wrote that it had carved its channel through 183 m (600 ft) of "sand benches to bed rock." The height and regularity of these flights of beaches suggest that they represent the higher levels of Lake McConnell, and that they might be contemporaneous with those located by Craig at 282 m (925 ft) above sea level. If so, this is evidence that all of Great Slave was free of ice at this time, which we have estimated to be about 8560 years ago (see below).

No long series of beaches like those below the highest shores of Lake McConnell have yet been described anywhere in the Mackenzie drainage basin except around Great Bear Lake. Their absence from the shores of Lake Peace and the higher shores of Lake Tyrrell suggests that these lakes were drained so rapidly that storm-built beaches could not be formed except during still-stands of the lake levels. Large deltaic deposits such as those in the Peace River valley indicate that such still-stands occurred, but their timing is obscure. Lake deposits that probably were formed in Lake Tyrrell were reported by Ells (1932) at an elevation of 427 m (1400 ft), or perhaps over 460 m (1500 ft), on the northeastern face of the Muskeg Hills. When these formed, the ice edge was at least 80 km (50 mi) northeast of McMurray (Taylor, 1960). It is also possible that the deposit represents one of the still-stands in the earlier drainage of Lake Tyrrell. Without more data on the rate and timing of isostatic rebound in this area this still-stand cannot be correlated with the deltaic features in the Peace River valley or elsewhere.

Noble (1971, p. 105, and pers. comm.) described an early Indian culture, called "Acasta Lake", in the region around the west shore of the north arm of Great Slave Lake, "...and thence northward, east of Great Bear Lake to within 70 miles of the arctic coast." A ^{14}C date of 7000 years B.P. was based on samples of charcoal from hearths used by people whose artifacts indicate that they were primarily forest dwellers. In this region, the evidence of culture was found at 14 sites on sand eskers or blowouts at elevations ranging from 259 to 427 m (850 to 1400 ft) above sea level. Noble

suggested that these people came into the area from the upper Mackenzie valley via the northwest shore of Great Slave Lake which, following Craig's interpretation (1965), would be Lake McConnell. There appears to be some cultural similarity between the Acasta Lake people and those represented by Millar's excavations near Fort Liard dated about 8700 years B.P. (Millar, 1968). These people probably travelled and camped on riverbanks and lakeshores where water and fishing were readily accessible, as do modern Indians in that country. The habit of camping on sand or gravel beaches around the eastern arm of Great Slave Lake was used by Noble (1971) as a way to check the chronology of the later cultural sequence for the region. This sequence was based on the study and comparison of archaeological sites, many of them having ^{14}C dates extending to the early 19th Century. The dates showed a regular progression from the oldest on the higher raised beaches to the most recent near the present level of Great Slave Lake.

The location of the lowest Acasta Lake site (259 m or 850 ft) is near the end of the North Arm of Great Slave Lake, at Mosquito Creek, just southwest of Frank Channel. It is about 80 km (50 mi) due south of the 282 m (925 ft) shoreline of Lake McConnell, located near Faber Lake by Craig (1965). About 7000 years ago it is probable that the Acasta Lake people traveled and camped on beaches that were then on a shore of the lake that was about 23 m (75 ft) below the uppermost shores noted by Craig. As the land continued to rise, later cultures used lower beaches as they were progressively formed and raised. If this concept is valid we may have materials with which to date the highest shores of Lake McConnell.

The rise of the land with respect to the lake level has been about 103 m (337 ft) in 7000 years (using 156 m (513 ft) as the present elevation of the lake). This gives an average rate of rise of about 1.5 m or 4.8 ft per century. Using this rate for the additional 23 m (75 ft) to the highest shores of Lake McConnell, the additional rise would have taken about 1560 years. Thus we have a tentative date for the beginning of Lake McConnell at about 8560 years B.P.

The proposed average rate of rise can also be used to approximate the time at which the Fort Smith escarpment became exposed and separated Lake McConnell into two lakes — Athabasca and Great Slave. The escarpment is now at about 205 m (675 ft) above sea level, so that at the highest level of Lake McConnell it would have been submerged about 76 m (250 ft). If the land rose at about 1.5 m or 4.8 ft per century, and if 8560 years B.P. is the approximate time of the formation of Lake McConnell, the escarpment would have emerged about 3350 years ago.

Again using 8560 years B.P. for the establishment of Lake McConnell, the propable upper and lower limits of Lake Tyrrell (534 m (1750 ft) and 282 m (925 ft) respectively), and the earliest date for Lake Tyrrell (ca. 10 000 years B.P.), then Lake Tyrrell would have been drained to the upper level of Lake McConnell (250 m or 825 ft) in about 1440 years. This gives an average rate of about 17.4 m (57 ft) per century. This cannot be a realistic figure because the time spans of at least two still-stands during which about 590 and 1150 km^2 (228 and 452 sq mi) of sandy aeolian and alluvial materials were accumulated in the Peace River Valley are unknown (Taylor, 1960). Therefore when the lake fell it went down far more rapidly than the average rate might indicate.

The available ^{14}C dates indicate that lakes formed in the basins of the Kazan, Dubawnt, Thelon, and Back Rivers were of relatively short duration. Craig (1959a, p. 510) from study of organic remains in a pingo in the Thelon basin (Lat. 64°17′, Long. 102°41′), concluded that the ice had left the site of the pingo "considerably more than 5500 years ago", long enough for the continental ice sheet to disappear, or to retreat to the ice divide and allow the proglacial lake to drain. Sorenson *et al.* (1971) found evidence that trees had reached north Ennadai Lake as early as about 6000 years ago, and Dubawnt Lake about 4000 years ago. It is possible that the proglacial lake in the Dubawnt basin was connected with that in the Thelon (Craig & Fyles, 1960, p. 8), at least in its early stages, and may have been drained as early.

Physiography of the Sandstone Areas South of Lake Athabasca

Tyrrell & Dowling (1897) described the region south of Lake Athabasca, underlain by Athabasca Sandstone, as a wide sandy plain, sloping gently downward to the north. Sproule (1939), using aerial photographs for reconnaissance, confirmed the plain-like character of the landscape. He mapped the southern boundary of the Athabasca Sandstone at about 208 km south of William

Point, Lake Athabasca. Recent contour maps (Energy, Mines and Resources Canada, 1:250 000, Sheets 74N, 74K, 74F) give the altitude of this point on the boundary at about 418 m above sea level. Thus, the general slope of the surface is about 98 cm per km. The sandstone beds are generally flat-lying though Blake (1956) reported some minor folding near Lake Athabasca. The weathering and glacial scouring of the sandstone appear to have produced most of the sand we see in the lake beaches and dune areas. Most of the local topography is formed of sandy glacial deposits variously reworked by wind and water.

Dowling ascended William River from its mouth at Lake Athabasca (Tyrrell & Dowling, 1897) and encountered the first rapids, composed of low sandstones ledges, about 19 km (12 mi) above the mouth of the river. He noted one fall of about 1.5 m (5 ft) and stated that the river fell only about 14.6 m (48 ft) in the 48 km (30 mi) that he travelled. Blake (1956), who descended William River, reported passing seventy-five rapids, most of which he associated with the passage of the river through morainic deposits. The sandy glacial drift is in the form of broad, gently rolling plains covered with jack pine or wide expanses of marsh and muskeg. Drumlins and eskers or elongated ridges are common, both are composed primarily of sand.

Tyrrell (Tyrrell & Dowling, 1897, p. 23D) described, in this region, a kind of morainic deposit which he considered distinctive:

"The most conspicuous and interesting drift hills in the whole region, however, occur in the basin of Cree Lake, around Black Lake and on the banks of Stone River. They are steep, narrow ridges, parallel to the direction of glaciation, with the sides joining in a crest that may be less than a yard in width. They average from a quarter of a mile to one mile in length, and round down gently to both ends, with a characteristic drumlin-like contour, and vary from 70 to 250 feet in height, the average being about 120 feet. Unlike eskers, or kames, which they resemble in some respect, they are not composed of assorted material, but rather of unassorted rock-flour mixed with boulders. Unlike drumlins, they do not seem to have been ever compacted or overridden by the ice, as the material is loose, and the summit is not rounded off from side to side, but rather from the crest downwards, they descend in as steep a slope as the material will stand at. Further, they all lie in the basins of large post-glacial lakes, the principal ones examined being in Hyper-Cree and Hyper-Black Lakes. As they seem to differ from any drift hills that have been definitely described, I would suggest for them the name ispatinow, the Cree word for a conspicuous hill."

He suggested that these "ispatinows" were formed in: "narrow gorges in the ice-sheet, when the front of the glacier was bounded by a deep lake. Streams flowing on or near the surface plunged into these ice-bound gorges and carried their load of detritus into the quiet water at the bottom of the gorge." He thought that the material would then remain unsorted. In more recent literature the ispatinows have been treated as elongated sandy drumlins (Flint, 1947, pp. 124-125; Charlesworth, 1957, pp. 390-423). The manner of their formation, however, is uncertain.

In his ascent of William River, Dowling (Tyrrell & Dowling, 1897, p. 70) described: "A boulder ridge, which seems to be beneath and protruding through the sands, crosses the river about nineteen miles above its mouth. The ridge is made up of more rounded material, and seems to be a continuation of a high ridge or series of long hills which lie to the east called the Fish Mountains. These hills are probably of the same character as the ispatinows around Cree and Black Lakes. Above the ridge the surface is more even and covered with a small growth of Banksian pine." It is presumed that Dowling's 31 km (19 mi) was measured along the river, and if so the ridge is about 4 km (2.5 mi) above the large William River dune area, at an altitude of about 275 m (900 ft) above sea level, and (according to the recent topographic map) situated in a broad sand plain partially covered with pine. Dowling (Tyrrell & Dowling, 1897, p. 70D) mentioned the "Fish Mountains" in one other place, at Beaver Point, where he said: "The country behind rises more abruptly. The Fish Mountains or Hills are seen as a wooded ridge 200 feet high above five miles inland, and are the edge of a higher plateau which gradually approaches the lake shore." Here he was looking across the Thomson Bay sand dunes which extend up to hills that are at 305–335 m (1000–1100 ft) above sea level.

The ridge mentioned by Dowling along William River was not seen by our field parties, but the hills south of Thomson Bay were examined in 1975. Close to the southern edge of the dunes is a prominent ridge made up of unsorted boulders, stones, and sand (Figure 26). About 1 km south of Little Gull Lake is another, more discon-

tinuous, east-west ridge located on a plain that rises only slightly to the south (Figure 6). It, also, is of unsorted coarse materials and sand.

East-west ridges of similar nature were examined by one of our field parties about 3 km south of the lake shore and about 8 km southeast of Wolverine Point. These ridges (Figure 14) are relatively straight for considerable distances, gegenerally parallel, but ocxcasionally forked and anastamosing. Many are discontinous and form series of ridge-like, variously separated, hills. The area lies between the 244 and 275 m contours, and the ridges are 9 to 12 m high with rather sharp summits.

In their orientation and altitudes the ridges near Lake Athabasca resemble the "ispatinows" of Tyrrell. They were almost certainly covered by a proglacial lake and have been greatly modified by wind and shore processes. These elongated ridges are important in the present context because they have a high content of sand which can be moved easily by wind or water.

No well-defined recessional moraines have yet been found on the area underlain by the Athabasca Sandstone. Sproule (1939) mapped a moraine to the southward and westward, extending from east of the Mudjatik River northwestward via the headwaters of the Gwillim River, Black Birch Lake, the upper Clearwater River, Lloyd, and Patterson Lakes. Small, parallel ridges northwest of Patterson Lake were considered recessional moraines. All of these are outside the south and southwest borders of the sandstone (Sproule, 1939; Blake, 1956).

In view of the preceeding suggested history of the sandstone region south of Lake Athabasca we propose that most of this region originated not as dry land exposed by withdrawal of glacial ice but rather as the predominantly sandy bottom of Lakes Tyrrell and McConnell. The former was drained relatively rapidly to form pronounced shoreline beaches only during still-stands of unknown duration down to about the upper level of Lake McConnell. At this level it might be called

Figure 6. Elongated ridge south of Little Gull Lake. The young jack pine seedlings, 6-11 years old, on the sand plain germinated after a burn.

"ancestral Lake Athabasca," with its southern shore extending eastward to the MacFarlane River and ranging from approximately the present 305 m (1000 ft) contour up to about the present 366 m (1200 ft) contour. It may have reached this level about 8560 years ago and possibly earlier. Since then, the rate of lowering has been much slower and more steady. The earlier drainage (251 m or 825 ft) may have lasted about 1440 years, while the later drainage (126 m or 414 ft) took about 8560 years.

It can be assumed that south of Lake Athabasca there is a series of beaches corresponding to those on the north side of the lake at Charlot Point. Judging by those recently formed on the present south shore, they are largely of sand, greatly accentuated by wave action and ice-push, and spaced at wide or narrow intervals depending upon the configuration of the shores along which they were formed and upon the position of these shores on a lake that was larger and stood at higher levels. They are probably highly altered in form by wind.

The best evidence we have of the nature of the surfaces thus exposed is the presence of ventifacts and sand polished cobbles and boulders in areas now stabilized by forest vegetation. Tremblay (1961) described this in an area between latitude 56° and 58°N, and between longitude 108° and 111°W. The localities studied are near Frobisher Lake in Saskatchewan and along the Marguerite River in northeastern Alberta. From Tremblay's description, they closely resemble the ventifacts we have found among the Lake Athabasca dunes and on forested sandy areas nearby. They presumably formed when there was not enough vegetation to obstruct the wind. The wind direction is shown by the orientation of the striation and fluting on bedrock. Both areas studied are outside the Athabasca Sandstone, but very near its southwestern boundary at altitudes over 488 m (1600 ft) above sea level. Tremblay (1961, p. 1563) stated: "These erosional features and some of the sand deposits in the form of dunes, sheets, and ridges, not described here, suggest that the area was a huge desert during or soon after the deglaciation, that the sand could move readily under the action of wind, that the vegetation cover was practically nonexistent, and that during a fairly long period there were strong winds blowing predominantly from southeast to northwest (ca. N. 35°W)."

In the area studied by Sproule (1939) he mapped, largely from aerial photographs, a great many long ridges generally trending at right angles to the northeast to southwest direction of ice advance. He described them (p. 104) as "narrow, generally sharp, ridges of sandy moraine... They pass over bare rock, and through muskeg, over hills and valleys, and are not deflected by surface irregularities. They vary up to three miles or more in length. The base width is seldom over 100 yards.... The highest measured was 35 feet. In most cases they are parallel to one another, although occasionally separate sets converge at acute angles." He believed them to be "ice-crack" moraines, formed in transverse cracks near the margins of receding glaciers.

David (1981) has recently studied much the same area seen by Sproule, but has greatly expanded the known occurrence of the long ridges, which he believes to be attenuated parabolic sand dunes. He mapped them as occurring not only beyond the sandstone area, but also well within it. He confirms the widespread presence of ventifacts and the southeasterly paleo-wind direction noted by Tremblay (1961). By studying the mean orientations of some 356 dunes over a distance of 275 km he found that their general southeast to northwest orientation gradually veered eastward about 9°. This suggested that the dune-forming southeast winds had had a curved trajectory, blowing clockwise around a center that lay to the eastward. He proposed that this center was in a high pressure system over what remained of the Laurentide ice sheet.

David (1981, p. 307) proposed that "dune activity in the Cree Lake region began perhaps around 10 000 years BP and lasted till about 8800 years ago" when the ice sheet had melted back far enough to greatly reduce the effects of winds from its high pressure system. He noted that the dunes are progressively less well developed eastward toward the MacFarlane and Cree Rivers, indicating gradual abatement of the winds. He thinks that by 8800 years ago the westerly, northwesterly, and northeasterly anticyclonic winds began to prevail. The date he has chosen for this change, 8800 B.P., is very close to the one we are suggesting (8560 B.P.) for the formation of Lake McConnell and the beginning of the slower and more steady rate of lake drainage by differential isostatic rebound. Also it probably dates the beginning of the present dune fields.

We are not able to judge whether Sproule or David is correct about the origins of these ridges; and if they are dunes, whether they may properly

be called parabolic dunes. In whatever way they are rationalized, they provide clear evidence that plant habitats of actively windblown sand probably have been widespread over one or another part of the Athabasca Sandstone area for at least 9000 years.

Geographic Distribution and Extent of Aeolian Sand in Northern Saskatchewan and Alberta and in the Continental Northwest Territories

Materials in this chapter are derived from our own field experience and from descriptions found in the exploration literature of the last two centuries. These descriptions will not be repeated here, but they may be found in the papers cited below. Notes extracted from them may be placed in four nonexclusive categories.

Sand plains — more or less level or gently rolling surfaces underlain by sand.

Sand hills or ridges — topography of sand not differentiated as having the forms of dunes, eskers, or drumlins.

Sand dunes — topographic forms clearly recognized as dunes.

Sandy eskers or drumlins — sandy ridges having the form and orientation of eskers or drumlins and recognized as such by the observers.

The following references are arranged in five geographic regions.

(1) Sand deposits in the drainages of the Athabasca, Peace, Buffalo, Hay, and Liard Rivers.

Allan & Carr (1946); Bayrock & Root (1972); Beach & Spivak (1943); Cameron (1922); Craig (1959a, 1959b, 1960, 1965); Craig & Fyles (1960); Day (1966, 1968); Hage (1944); Lindsay *et al.* (1958a, 1958b, 1960); Odynsky & Newton (1950). Odynsky *et al.* (1952, 1956); Rutherford (1930); St-Onge (1972); Taylor (1956, 1960); Williams (1922).

(2) Sand deposits bounded north by Athabasca and Black Lakes, west and south by the margin of the Canadian Shield, and extending eastward to Wollaston and Cree Lakes, Cree and Mujatik Rivers.

Alcock (1936); Blake (1956); Fahrig (1961); R. Green (pers. comm.); Sproule (1939); Tremblay (1961); Tyrrell & Dowling (1897); David (1981).

(3) Sand deposits between Lake Athabasca and the eastern arm of Great Slave Lake.

Blanchet (1926b); Camsell (1916); Wilson (1939).

(4) Sand deposits in the country between Great Slave and Great Bear Lakes.

Noble (1971, 1974); Preble (1908); Stockwell (1933); Thieret (1964).

(5) Sand deposits in the region northeast and east of Great Slave and Great Bear Lakes, including the drainage basins of the Kazan, Dubawnt, Thelon, Lockhart, Back, and Coppermine Rivers.

Anderson (1940-41); Back (1836); Bell (1901); Bird (1951); Blanchet (1926a, 1930); Craig & Fyles (1960); Hanbury (1904); Harp (1961); Hearne (1796); Kidd (1932, 1933); McDonald (1926); Porsild (1929); Richardson (1823); Taylor (1960); Tyrrell (1898); Wilson (1939, 1945).

The places of nearly all observations recorded in the above literature can be located with fair precision on a modern map. When this is done, a pattern for the distribution of aeolian sand becomes apparent although there are large areas that are relatively unexplored.

A major boundary follows the north northwest – south southeast trend of the division between the Canadian Shield and the softer rocks that lie west of it. In the west the glacial drift is relatively fine textured and is derived mainly from Paleozoic or Cretaceous shale, gypsum, and limestone. Aeolian sands are confined mainly to deltaic deposits in the broad valleys of the larger streams.

East of the boundary, on the harder rocks of the Canadian Shield, the drift is mainly of sand and gravel with far more boulders. Where the surface rock is granite, gneiss, or of crystalline, highly metamorphosed Archaean sedimentary rocks, the drift is thin, bouldery, and gravelly. Where the surface rock is sandstone the drift is mainly of sand and is usually much thicker. This contrast was noted by Sproule (1939) in the country west of Cree Lake, and by Wilson (1939) northeast of Great Slave Lake.

The major areas of aeolian sand in the Canadian Shield portion of the region are the areas where the drift is directly underlain by sandstone. A map of the aeolian sands made from the sources listed above is generally coincident with Fahrig's map (1961) showing the distribution of sandstone (Figure 2, with modification). The movement of the Keewatin ice sheet was toward the west and the sandy drift was transported in this direction from its sandstone sources. Hence the western borders of the aeolian sands extend beyond the borders of the sandstone areas. This was noted by Wilson (1939) when he found the sands northeast of Great Slave Lake to be progressively thicker eastward

toward the sandstone areas of the Thelon basin. It was also seen by Tremblay, (1961), Sproule (1939), and David (1981) who saw dune topography, ventifacts, and wind-cut rock outcrops beyond the western border of the sandstone south of Lake Athabasca.

From Bird's map and descriptions we estimate that at least 50 percent of his area has very sandy drift which has been or is now being reworked by wind. Sproule's map and photographs, as well as his text, indicate that at least the southern part of the Athabasca Sandstone area is a sandy plain whose relief is mainly formed by eskers and drumlins that are also made up primarily of sand. Blake's notes (1956) corroborate this and carry it northward to Lake Athabasca. In view of Tyrrell's descriptions of the region of Cree River and Black Lake, it seems reasonable to assume that at least 80 percent of the Athabasca Sandstone area may have gone through a period of intense aeolian activity. Sandstone underlies only a part of Taylor's map area but his notes on the nature of the drift suggest that about 60 percent of his area is or has been subjected to reworking of sand by winds. An estimate for Wilson's map areas (1939, 1945) has to be based largely on observations by earlier students. All the eskers he mapped were believed to be of sand. Blanchet's description of a great sand plain between Artillery and Ptarmigan Lakes (1924-1925) suggested that even in the western parts of Wilson's map areas there are large tracts of sand, exclusive of the eskers, that have been reworked by wind. We estimate that at least 75 percent of his map areas may be so classified.

An estimate of the total area of windblown sand in the region is bound to be speculative. The figures given below are conservative and tend to be under-estimates rather than over-estimates. The most reliable data are for the deltaic deposits in the valleys of the major rivers west of the Canadian Shield — the Athabasca, Peace, Slave, Liard, and upper Mackenzie Rivers. They are based on soil or hydrographic survey maps by Day (1966, 1968), Lindsay *et al.* (1958a, 1958b, 1960), Bayrock & Root (1972), and on St-Onge's (1972) maps of postglacial lakes in the upper Athabasca basin. Together they total approximately 20 453 km^2. In the Canadian Shield portion of the region the total area of the mapped surface deposits of sandstone is estimated roughly at 209 062 km^2.

We have four maps on which glacial features are given in some detail, two located mainly in sandstone areas and two on areas marginal to the sandstone. Bird (1951) mapped about 53 075 km^2 in the Thelon River sandstone region and Sproule (1939) about 13 986 km^2 around Cree Lake and northwest of it. Wilson's maps of eskers (1939, 1945) cover about 89 870 km^2 in the Lockhart basin and eastward to the upper Thelon. Taylor's (1956) map of a portion of the Middle Back River comprises about 16 316 km^2.

The above estimates do not do justice to large areas of sandstone, such as those along the Arctic coast and along the Snowdrift River, for which we

Table 2 — Distribution of Sand and Aeolian Activity in Northern Saskatchewan and Alberta and in the Continental Northwest Territories

	Total area in km^2	Probable percent of area subject to aeolian activity	Probable area subject to postglacial aeolian activity in km^2
Cree, Athabasca, Black Lakes region	71 900	80	57 520
Thelon River region	64 800	50	32 400
Arctic Coast region	66 000	50	33 000
Snowdrift River region	6500	50	3250
Esker region NE of Great Slave L. (Wilson)	90 000	75	67 500
Middle Back River region (Taylor)	16 400	60	9840
Athabasca and Peace River region	20 500	100	20 500
Slave, Liard, and Upper Mackenzie R. region	2100	100	2100
TOTALS	338 200		226 110

have inadequate information. Furthermore, the 50 percent figure we are using for these and the large Thelon area based on the "sample" provided by Bird, is probably much too low. Table 2 is a summary of the above estimates.

The Advance of Forests and the Postglacial Xerothermic Period

Stabilization of aeolian sand in our region is accomplished by the development of vegetative cover, the most effective being forest and muskeg. Both the advent of vegetation and the movement of the sand have, in turn, been conditioned by the postglacial warm-dry, or xerothermic period (called by some authors the "hypsithermal" period).

The Trees

The poplars were the first trees to move into the western interior of Canada (Lichi-Federovich, 1970) and into the subarctic (Ritchie, 1977). The poplar woodland, however, formed a very short phase immediately preceding the invasion of spruce (Ritchie & Yarranton, 1978). White spruce (*Picea glauca*) is, primarily, a tree of medium to well drained soils, while the black spruce (*P. mariana*) is most characteristic of poorly drained soils such as develop on muskegs or over heavy clays. These are by far the most abundant trees in the boreal American forests. Less abundant, and of less continuous distribution are tamarack (*Larix laricina*) and white birch (*Betula papyrifera*), both of which are sometimes found with the spruces at or near the arctic tree line. Somewhat more southern in the boreal forest are the pines (*Pinus contorta* and *P. banksiana*), balsam poplar (*Populus balsamifera*), trembling aspen (*P. tremuloides*), and the firs (*Abies lasiocarpa* (Hook.) Nutt. and *A. balsamea* (L.) Mill.).

The white spruce, *Picea glauca* (s.l.) now ranges throughout the boreal American forest, from Newfoundland to western Alaska and southward into northern New England, and the northern Cordillera. The black spruce, *Picea mariana*, also

Figure 7. Beach ridge on the Lake Athabasca shore. *Picea glauca* var. *albertiana* is the primary tree on the ridge and *Elymus mollis* appears on the beach dune.

has a wide trans-continental range but it differs somewhat from that of *P. glauca*. In the Appalachian Mountains it reaches considerably farther south than the latter, and in interior Alaska, central and southern Yukon, and in southwestern Mackenzie there appears to be a large area in which it occurs sparingly or not at all (Hultén, 1968, p. 62). There is an area around Kluane Lake in southwestern Yukon where it is not found, and where its place in the muskegs is occupied by the ubiquitous white spruce.

These species probably had similar ranges in pre-Wisconsin time, and perhaps in earlier interglacials. During long periods they had large, continuous populations. In white spruce there developed regional ecotypes that were genetically segregated and were adjusted to major habitat complexes (LaRoi & Dugle, 1968). These habitats varied from south to north and from east to west. Strains were developed in the northern Rocky and Mackenzie Mountains and in Alaska adjusted to the subarctic-montane conditions of those regions. In both the western and eastern segments there probably were "clines" of ecotypes ranging from those adjusted to subarctic habitats to those living in more temperate regions. The occurrence, in *P. glauca*, of photoperiodic ecotypes that evolved as adaptations to northern climates (seasonally changing environments) was demonstrated by Vaartaja (1959).

The black spruce appears to be remarkably uniform taxonomically throughout its wide range. No morphological subdivisions such as occur among the white spruces (see below) have ever been defined. There seems no doubt, however, that its population has contained ecotypic variations analogous to those in the white spruce and of many other common species.

The major effect of the Wisconsin glaciation upon these patterns appears to have been the destruction of major parts of them (Hultén, 1937). The ice completely separated the continent-wide, continuous populations into eastern and western segments, and at the same time reduced the

Figure 8. The columnar habit of *Picea glauca* var. *albertiana* as shown by trees growing near treeline at Fairchild Point, Great Slave Lake, N.W.T.

segments to smaller or larger fractions of their former extent. The remains of the northwestern populations are thought to have lived through the Wisconsin glaciation in central Alaska, or in the eastern foothills of the Rocky and Mackenzie Mountains and perhaps in the Richardson Mountains. The eastern and central segments were reduced to scattered populations south and southeast of the ice. Subarctic ecotypes that formerly ranged through the northern parts of the eastern populations must have been nearly or quite completely eliminated, leaving only the ecotypes that were adjusted to life at or near the southern borders of the former range of the species.

Trees coming into our region after the Laurentide ice receded, therefore, are believed to have migrated from these remnant populations (Hultén, 1937; Halliday & Brown, 1943; Raup, 1930, 1946).

The most common white spruce in northwestern Canada north of about the 60th parallel is var. *albertiana*[2], a tree with a narrowly pyramidal or columnar crown (Figures 7 & 8) and cones that are shorter and broader than those of the eastern white spruce.

Hultén (1968, p. 61) stated that var. *albertiana* replaces the typical eastern *P. glauca* var. *glauca* "from Keewatin and northern Saskatchewan west." The late A. E. Porsild (pers. comm.) pointed out that part of this replacement is made by another segregate of *P. glauca*, var. *porsildii*, a tree that resembles the eastern white spruce in form but is readily distinguished by relatively smooth bark that has resin blisters like those on the balsam fir. It is common in the Mackenzie valley and extends westward through Yukon to central Alaska. Some of the white spruce in the southern part of the Mackenzie drainage basin, northward to the lower valleys of the Athabasca and Peace Rivers and along the upper Slave River are more broadly pyramidal than var. *albertiana* and may represent the typical *P. glauca* of the eastern boreal forests.

The white spruce appears to have been the principal coniferous tree in the advance of forests in northwestern Canada and Alaska following the retreat of the last glacial ice. It is the tree of most of the arctic timberline in this region and probably was the first to reach it. The following discussion, therefore, will be concerned mainly with this species.

[2]The name var. *albertiana* may not be available for this common tree if it is proved to be based on a hybrid between *P. glauca* and *P. engelmannii* Parry as suggested by Taylor (1959), Horton (1959), and Roche (1969).

The Probable Pattern and Chronology of Advance

A general pattern for the advance of forest into the glaciated region probably was the same as that we see now at boundaries between major types of vegetation. Such boundaries usually form a dendritic pattern that follows that of the drainage systems that cross the boundary. The largest example we have of this is the boundary between the deciduous forests of the Mississippi valley and the grasslandof the Great Plains. The streams are bordered by forest for hundreds of kilometers to the westward, while the interfluves are open grassland. The long westward extensions of trees are called "gallery forests." The arctic timberline has the same general pattern. Such gallery forests form projections into the tundra in the valleys of the major streams. The longest extensions are in the streams flowing northeast or north: the Thelon, Coppermine, and Mackenzie Rivers. Shorter ones extend upstream from the large lakes: the Snare and Dease Rivers are examples. The Back River has no gallery forest, for it rises in the tundra.

Using the above sketch, it is possible to outline a probable history for the advance of forest into our region (Table 1). Before the advent of the Pleistocene glaciation, the great rivers from the western mountains, the Athabasca, Peace, and Liard, had already carved deep valleys in the adjacent High Plains. These valleys broadened outward as the plains lowered to the east and were separated by wide interfluves with gently rolling surfaces. As the glacial ice receded and the postglacial lakes were drained, these plains probably became covered rapidly with some form of tundra or grassland, or some combination of the two. Drainage of the plains probably was imperfect, so that both wet and dry grassland or tundra sites were widespread. Probably dry sites were relatively more prevalent than would be the case today because of the developing xerothermic climate. It is probable that trees came into the delta region of the Mackenzie River and into its lower valley fully as early as those in the upper Peace and Athabasca valleys or perhaps earlier, coming from the eastern slopes of the Mackenzie and Richardson Mountains. Trees from the eastern remnants of the

boreal forest apparently reached the southern part of the Mackenzie basin somewhat later, possibly via the Churchill River valley.

A tentative chronology for the advance of forest into our region can be approximated from the ^{14}C dates that are available. The principal sources for these dates are in reports of palynological and archaeological research. Ritchie (1972, 1977) and Ritchie & Lichti-Federovich (1967, 1968) have described the hazards attendant upon the interpretation of pollen stratigraphy in the Arctic and Subarctic, especially in the absence of macrofossil material. This is due to several causes, not the least of which is long-distance aerial transport of pollen. They cite the case of the current pollen rain at Resolute on Cornwallis Island in the Arctic Archipelago, where 60% is composed of *Picea*, *Pinus*, *Betula*, *Populus*, *Juniperus*, *Alnus*, and Ambrosiae, all of which had been transported at least 1500 km. In our use of ^{14}C dates, therefore, we have depended mainly on those supplied from macrofossils.

Our conception of the late- and postglacial history of the spruce forests raises several questions that should be dealt with before any elaboration is attempted. Is there clear evidence that white spruce survived the last ice advance in the refugia mentioned above? If so, were the surviving populations large and varied enough to have maintained their habitat versatility? Was there an ice-free corridor of sufficient continuity in the eastern foothills of the Rocky, Mackenzie, and Richardson Mountains to have harbored such a population?

Hultén (1937) considered the Yukon valley in Alaska a viable refuge for a large area of boreal forest during the Wisconsin glaciation. Hopkins (1972) attests to its being unglaciated, but restricts the spruce refuge to a relatively small area near the mouth of the Yukon River (pp. 136-137). Although the temperature climate he proposes for the period would have permitted forests farther east, he thinks lack of moisture would have precluded them. He proposes that central Alaska got its present spruce from the small lower Yukon refuge and from south of the Laurentide ice sheet in Montana and Alberta (p. 141), presumably by way of the Mackenzie valley.

The assumption that spruce bordered the last ice in Montana and Alberta is of longstanding. The ice in this area presumably had encroached on the grassland of the Great Plains, with spruce migrating ahead of it to become the remnant population from which it later migrated northward to the lower Mackenzie valley and thence to central Alaska, a distance of at least 3200 km. Whether such a refugium actually existed in Alberta and Montana has been questioned (Raup, 1946, pp. 77-78), but if it did it probably would have consisted of spruce containing only southern ecotypes incapable of that long expansion to the arctic coast. An analogous situation may be that of the small spruce population placed by Hopkins near the mouth of the Yukon. If the interglacial forests of central Alaska were completely eliminated during the last glaciation, the remnant on the more humid west coast may not have been versatile enough to move into the drier interior as rapidly as Hopkins suggests.

The preceding notes suggest that the most likely source for the postglacial spruce in our region is in the northern Cordillera, probably in the eastern valleys and foothills. Much turns upon whether there actually was a "corridor", in the Mackenzie River region between Cordilleran and Laurentide ice during the last glacial maximum. Many archaeologists have assumed or hoped that there was, for it would provide a much-needed late glacial route by which people coming through northern Beringia could reach the northern Great Plains. But many geologists have been loath to accept such a corridor, and argument over it still goes on.

There seems to be no question that the Mackenzie River was stopped during the last ice advance. Otherwise the great proglacial lakes could not have been formed in the central part of the basin. It also seems clear that the ice receded first from the Mackenzie delta region and the lower Mackenzie valley (Craig, 1965.)

According to Prest (1969) the ice began to leave the delta region 13 500–14 000 years ago. Ritchie & Hare (1971) presented evidence that the first tundra vegetation appeared on the Tuktoyaktuk Peninsula, just east of the mouth of the Mackenzie, about 12 900 years ago, and that spruce came about 11 500 years ago, forming an open forest-tundra vegetation. Ritchie (1977), working on the Campbell-Dolomite uplands near Inuvik on the east side of the delta, found that poplar appeared about 10 300 years B.P. and spruce about 10 000 B.P. He thought that this spruce came from southeastern refugia after the Mackenzie valley became ice-free. Mackay and Terasmae (1963) described driftwood from a pingo among the Eskimo Lakes east of the Mackenzie delta dated at 10 800 B.P. Müller

(1962, p. 262) found driftwood at a pingo near Tuktoyaktut dated about 12 000 years ago.

Mackay & Mathews (1973) in a study of the geomorphic development of the Mackenzie River valley in the vicinity of Good Hope, described a section of deltaic and floodplain sediments that had been deposited in a lake probably held up by an ice dam in the main drainage line of the Mackenzie River below Good Hope. Water supplying this lake came "from the southwestern edge of the Mackenzie plain... via Mountain River," which rises in the Mackenzie Mountains. Deposits in the bottom of this lake (wood), gave an age of 11 000 to 11 500 years B.P.

These data indicate that postglacial driftwood was coming down the Mackenzie River from somewhere above Good Hope, either from the Mackenzie itself or from the Mountain River. Prest's estimate (1969) for the opening of the Mackenzie valley drainage about 10 000–11 000 B.P. suggests that the wood may have been coming from both sources. If so it could have originated in the Liard River valley or from several other western tributaries of the Mackenzie. It is virtually certain that little or none of the early driftwood found in the delta or around Good Hope could have come from the southern parts of the Mackenzie drainage basin, to say nothing of deriving it from the assumed refugium in Alberta and Montana. Any that might have come out of the upper valleys of the Athabasca, Peace, Hay, or Buffalo Rivers would have been caught in the great lake that lay in the valleys of these rivers and in the basins of the present large lakes.

We believe it reasonable to suggest therefore that populations of spruce probably lived through the last glaciation in the eastern valleys and foothills of the mountains west of the Mackenzie River. The forest may have been patchy in places or open forest-tundra, but probably there was no large discontinuity.

All of the earlier proposals for the postglacial origins, migrations, and chronologies of these forests were made without regard to the differences among the white spruces. We can only suggest the effects of these differences, using what we know of the present ranges of the varieties of white spruce, and of their probable behavior since the disappearance of the last glacial ice.

We presume that the populations on the eastern slopes of the mountains were of Alberta spruce (*Picea glauca* var. *albertiana*) with its array of ecotypes nearly or quite intact. When the Tuktoyaktuk Peninsula was free of ice with tundra established, this spruce would have been nearby and already adjusted for a forest–tundra habitat. It then began a long migration eastward and southeastward, forming the arctic timberline and the subarctic open park-like forest.

We have already noted the archaeological findings of Noble (1971, 1974) in the region northeast of Great Slave Lake, where an Indian culture was dated at about 7000 B.P. He also found charcoal in the soils that he could interpret as evidence of "natural" forest fires. His oldest date for burned forest (6900 years B.P.) came from the Snare River gallery forest area as did also his next oldest date (about 5089 years B.P.). This spruce probably migrated eastward from the Mackenzie valley by way of the Bear River and the shores of the Great Bear Lake, or via the northwest shores of ancestral Great Slave Lake.

We have not seen the gallery forest that extends northeastward in the Thelon River valley, but judging by photographs of white spruce there, published by Clarke (1940), it also is var. *albertiana* and closely resembles that found at the eastern end of Great Slave Lake (Figure 8). The headwaters of the Thelon are not more than 20 km from the site of the photograph in Figure 8. A photograph published by Blanchet in 1926a shows the same spruce growing among the Thelon headwaters.

Gordon (1975) proposed that trees first came into the upper Thelon valley not long after 6000 years B.P. and that forest advanced down the Thelon in a later expansion. He dated an arctic culture on the Thelon between 3200 and 2900 years B.P., the excavations of which contained macrofossils of black and white spruce and tamarack. Gallery forest along the Thelon presently constitutes its longest extension into the tundra in western Canada. It was mapped by Rowe (1972) as an isolated "island" rather than an extension and is about 200 km long. It may be a relict from a former extension, perhaps a remnant of the first great expansion of forest which successfully weathered subsequent colder periods.

Terasmae & Craig (1958) discussed the ecological and climatological significance of fossils of *Ceratophyllum demersum* L., a species now limited to a more southern range, and rather abundant pollen of spruce and pine, in a pingo in the Thelon valley (Craig, 1959). The authors (Terasmae & Craig, 1958, p. 568) say "the evidence seems to indicate that the silt was deposited during a

postglacial climatic episode warmer than the present, the postglacial thermal maximum. [It was found to have a ^{14}C date of 5400 ± 230 years B.P.] The formation of the pingo is necessarily a later event and may coincide with the marked cooling of climate following the postglacial thermal maximum." If Gordon is correct in having trees along the upper Thelon soon after 6000 B.P., spruce should have been there to contribute its pollen. But the pine is a somewhat more southern species in the boreal forest (Raup, 1933a, 1946). Considering the findings of Ritchie and Lichti-Federovich (1967, 1968) on the long-distance transport of pollens, pine pollen in the pingo silt does not prove that the pine was growing there at the time of deposit.

We know from Noble's dates for burned forest (1974) that the spruce was in the country northeast of Great Slave Lake about 7000 B.P. By air line this is about 1100 km from the Tuktoyaktuk Peninsula where it first appeared about 11 500 years ago. A very rough estimate of its migration rate is therefore about 0.24 km per year. Hopkins (1972, p. 141) stated that spruce first appeared in the Tanana valley of central Alaska about 8000 years ago. If it came from the Mackenzie delta region it had migrated some 880 km in about 3500 years. This is approximately the same rate, 0.25 km per year, that it showed in its easterly extension. The eastward migration must have followed the recession of the ice rather closely, for the latter is thought to have disappeared from Keewatin not later than 7000 years ago (Craig & Fyles, 1960; Prest, 1969).

These long migrations are, in themselves, evidence that the Alberta spruce came through this last glaciation as a versatile, plastic taxon, relatively rich in biotypes, which suggests that its population in the northern mountains had not been greatly reduced.

Following the general pattern of gallery forest advance, we assume that the first routes by which forests followed the ice retreat into the central part of the Mackenzie were down the valleys of the Athabasca, Peace, Liard, and other rivers flowing eastward from the mountains. The first white spruces in these valleys would have been var. *albertiana* with ecotypes which, from south to north, probably were progressively adjusted for life in boreal forest habitats. Evidence for this is found not only in the presence of the Alberta spruce in the existing flora of the Athabasca–Great Slave Lake region, but also of many other taxa of woody and herbaceous plants whose geographic affinities are in the western mountains and foothills (Raup, 1946, pp. 63-78).

The warming trend in the climate, together with abundant moisture in the valley bottoms, would have favored rapid migration downstream. The invasion of the central part of the Mackenzie basin was delayed during at least two still-stands in the drainage of the postglacial lakes down to the level of Lake McConnell. It is possible that migration occurred around the shores of the lakes, but, if so, the process would have been hazardous because of steady or episodic adjustments of water tables.

A pollen profile of sediments from Lofty Lake in the upper Athabasca River region (Lichti-Federovich, 1970) shows a sequence somewhat different from that of Ritchie & Hare (1971). Lofty Lake is on the upland, 52 km from the Athabasca River. The base of the core, representing a *Populus–Salix–Shepherdia–Elaeagnus–Artemisia* forest–shrub vegetation, was dated at 11 400 years B.P. The poplar was replaced by spruce (6000–5700 B.P.) and other boreal forest trees which continue to the present. *Populus balsamifera* and *P. tremuloides* commonly occur along water courses (Jeffery, 1961) and their appearance here may represent the beginning of gallery forest along streams. The late appearance of spruce on the upland may reflect the probable tendency (discussed below) for the interfluves in this region to remain in some form of tundra or grassland long after the gallery forests had developed.

We do not know when forest first came into the Cree Lake or Reindeer Lake regions, nor do we know whether the white spruce was of the eastern or western form. The eastern white spruce, *Picea glauca* var. *glauca*, having no subarctic ecotypes left in its populations, had to make new adjustments as its migration took place northward and northwestward. Possible routes for it into our region may have been up the Churchill River to Cree Lake or via the lakes and streams of the old fur trade route to the Clearwater River. At some time it accomplished this, for trees closely resembling it are now found along the lower Athabasca River where it grows with the balsam fir which is more southern in the boreal forest and not found north of the Athabasca delta. Whether it was ever able to produce a northward extension to Dubawnt Lake we do not know. If it did, it migrated much more slowly than did the Alberta spruce in its long migration eastward from the Mackenzie (see below).

Recent work on the tree line has been done on archaeological problems in the Dubawnt, Thelon, and Kazan river systems. The tree line has long been recognized as a major cultural boundary between the people of the Arctic and the Indians of the boreal forest. Archaeological excavations have shown clear shifts in the cultural boundary during postglacial time, with southward advances and northward retreats of the arctic culture. For details of this research, the reader is referred to the following papers: Bryson, *et al.* (1965); Dennis (1970); Gordon (1975); Larsen (1965); Lee (1959); Nichols (1967a, 1967b, 1967c, 1969, 1970); Sorenson, *et al.* (1971); Terasmae (1961, 1967); Terasmae & Craig (1958). Most of the material in these papers is summarized by Gordon (1975). Evidence of former extensions of forests into the tundra rests not only on fossil pollen (Nichols, 1967a, 1967b) but also on forest soils now found as palaeosols in the tundra beyond the present limit of trees (Bryson, *et al.*, 1965); Larsen, 1965).

The earliest of the palaeosols, and the farthest north in the Kazan drainage, was dated about 6000 years B.P. This site was at the north end of Ennadai Lake. The earliest in the Dubawnt drainage at Dubawnt Lake was at about 4000 years ago. It is stated by Gordon (1975, p. 35) that no charred podsols were found at Marjorie or Grant Lakes, indicating that these lakes, some 120 km northeast of Dubawnt Lake, had never been south of the timberline.

Beginning somewhere in the country east of the east end of Great Slave Lake the black spruce gradually replaces the white spruce as the principal timberline species. Gordon (1975, p. 48) states that "*Picea mariana*, and to a lesser extent *Picea glauca*... comprise the dominant modern upper Thelon River vegetation. They extend from Eyeberry to Beverly Lakes, a river distance greater than 150 miles." The last woods seen by J. B. Tyrrell (1898) on his journey down the Dubawnt River was a short distance south of Dubawnt Lake and was of black spruce. Baldwin (1951) noted black spruce as the primary species of this genus at or near timberline at Nueltin Lake. Rowe (1972) makes it the principal timberline species in northern Quebec. It may be that the eastern spruces, white or black, reached the timberline at Dubawnt Lake long after the Alberta spruce had got nearly to Beverly Lake, about 160 km farther into the tundra. This may be, in part, because they may have come from eastern refugia and had lost their subarctic ecotypes in the Pleistocene devastation.

The rate at which the interfluves were forested can only be surmized. The gallery forests probably were confined mainly to the valleys for a long time. The adjacent uplands seem to have become progressively drier until the close of the xerothermic period 5000–6000 years ago. This would have favored the persistence of grassland or the drier forms of tundra.

Natural grasslands are now of wide occurrence throughout the uplands west of the Canadian Shield. In modern times those in the upper Peace River region and southward have become farmlands. Northward they extend to the upper Mackenzie valley. A reasonably good map of the distribution of these grasslands can be made from the range of the bison as it was known within historic times (see Raup, 1933b, and Soper, 1941 for details of the former range of the bison). It was found throughout the uplands adjacent to the Athabasca, Peace, Hay, Buffalo, and Liard Rivers and it was along the Mackenzie River at least as far north as Fort Simpson, and northeastward adjacent to the base of the Horn Mountain plateau.

Mackenzie (1801) reported a tradition among the Indians he met near the junction of the Peace and Smoky Rivers in the winter of 1792-93. They told him that the neighboring hills and plains, at that time grasslands interspersed with groves of poplars, were formerly covered with moss, and without any large game animals except caribou. Gradually the country changed to its present appearance, the caribou disappeared, and were replaced by elk and bison. Something like this must have happened in this area during the period between the disappearance of the ice and the closing centuries of the xerothermic period. Since then the bison and its range have dwindled to the smaller numbers of animals scattered through the prairie openings found by Europeans when they came into the country in the 18th and early 19th Centuries.

The aforestation of the interfluves of the Precambrian country may have been a somewhat slower process than it was west of the Canadian Shield boundary. There are no well-organized drainage systems on the crystalline rocks of the higher parts of the plateau. Rather, the major streams flow through mazes of lakes and are fed by innumerable small tributaries. Glacial drift in this rocky country is so scant that there is little continuity in riverine deposits that would support gallery forest. The presence of elaborately anas-

tomosing waterways, on the other hand, may have favored slow advance on a broad front.

The Advance of Forest South of Lake Athabasca

In areas underlain by the Precambrian sandstones, the glacial drift was relatively thick. Rivers and lakes were commonly bordered by sandy terraces or beaches along which gallery forests could have advanced more rapidly. Thus the Cree, MacFarlane, and William Rivers, flowing northward over the Athabasca Sandstone to Athabasca and Black Lakes, may have developed gallery forests rather rapidly.

The only ^{14}C date we have for early forest in the Athabasca lake dunes is from charcoal found by Hermesh (1972, and pers. comm. 1977 & 1978) on what he thought to be a raised beach west of Yakow Lake. The charcoal was dated at 4920 ± 60 years B.P. (Rutherford *et al.*, 1975). The charcoal was from beds of sand that could be distinguished from each other by slight differences in texture or compaction. These beds sloped 30° north. The charcoal included, "numerous chunks—some fairly large—1-3 cm. dia." and appeared as lines across the surface of the ground. Apparently the wood was not identified.

The form and position of the beds suggest that the charcoal was transported and deposited by water or wind. The exposure is near the delta of the MacFarlane River which may have brought the charcoal to the lake where it may have floated to nearby beaches. If so, it could have come from anywhere on the banks of that river, the headwaters of which are not far from Cree Lake. If carried by wind, it could have been deposited at intervals on the slipface of a dune, alternating with layers of sand. If our reconstruction and dating of the Lake McConnell shores in this area are even approximately correct the site of the charcoal (now at ca. 275 m above sea level) was at about 213 m above sea level about 3500 years ago. The elevation and date are close to those we have estimated for the emergence of the Smith Rapids escarpment. The date suggests that the charcoal was redeposited because it is much older than the site in which it was found.

The only other ^{14}C date we have for the dune area is much younger 770 ±80 years B.P. (Lowdon & Blake, 1980). It was based on charcoal of *Pinus banksiana* collected by one of our parties in 1975 in the Thomson Bay dune area (Lat. 59° 03′ Long. 109° 00′) near an elevation of 275 m. The material was in large pieces, found lying on sand and covered by about 13 cm of sand over which was a single layer of small stones. The deposit probably represents a process that is now current in the dune area—burial of pine forests by blowing sand, in this case possibly by blowouts following the exposure of the sand by the fire that produced the charcoal.

It is notable that, in spite of the many traverses that have now been made through the Athabasca dunes and over the gravel plains scattered among them, and in spite of the many pits that have been dug in them, the only ancient charcoal that has been found is that collected by Hermesh near the lower MacFarlane River. If the earliest trees to come into this region formed a gallery forest along the valleys of the larger streams and left the interfluves open, as we suggest, then the remains of forests would most likely be found along the streams and in their deltas.

David (1981, pp. 306-308) has proposed that the Cree Lake dunes became stabilized by vegetation when the northerly winds replaced the southeasterlies about 8800 years ago. He suggests that stabilizing vegetation came very soon after that date, but whether it included trees we do not know. The principal species now seen in the area, judging from his photographs, is jack pine except in wetlands where black spruce and/or tamarack are evident. Even with the change of winds this sandy country must have been very dry, for the xerothermic period was building up toward the maximum which came 2000–3000 years later. It seems more likely that neither pines nor white spruce came to the interfluves until the close of the xerothermic period. The pines are obviously still unable to grow on the barren tops of the ridges.

Suggested Times of Aeolian Sand Activity

From our hypothesis that the advance of forests into most of the region was by gallery extensions in stream valleys, it follows that the adjacent uplands were open for the movement of sand deposits by wind long after trees had reached the central part of the region. The vegetational contrasts formed in this way probably were greatly accentuated by the warmth and dryness of the xerothermic period.

The exposure of land surfaces between the Canadian Shield boundary and the Rocky Moun-

tains was progressive from west to east due to the drainage of postglacial lakes Peace, Tyrrell, and McConnell, interrupted by still-stands of unknown length. We have derived a tentative date for the formation of Lake McConnell at about 8560 years B.P. (Table 1).

Judging by present-day elevations and estimated times, the lowering of Lake Peace may have been at an average rate of about 12.2 m per century, and Lake Tyrrell at about 17.4 m per century. Though these rates are speculative, the estimated rate for Lake McConnell is conspicuously slower: about 1.46 m per century in the north arm of Great Slave Lake. Using the same assumed elevations and times, land exposed by the drainage of Lake Peace would now be between 13 500 and 10 000 years old; by that of Lake Tyrrell between 10 000 and 8500 years old; by that of Lake McConnell to the separation of Athabasca and Great Slave Lakes between 8500 and 3300 years old; and by that of the present Mackenzie lowland below the Fort Smith escarpment between 3300 years old and the present.

The upland glacial drift west of the Canadian Shield boundary, which consists of fine-textured materials, has not been as susceptible to aeolian influence as that east of the boundary. With its much greater water-holding capacity, it was soon able to support denser vegetation. Nonetheless, it probably was restricted for a long time to some type of tundra or tundra grassland, much of which still persists as prairie openings in the boreal forest of the region.

Wherever there were deltaic or lake beach deposits reworking by wind was active. Most higher level deposits probably came into existence during the drainage of Lakes Peace and Tyrrell, between 13 000–14 000 years and about 8560 years ago; larger ones at lower elevations probably appeared in the last ±8560 years during the formation and drainage of Lake McConnell. The complete distribution of deltas in the region is unknown, those that have been mapped total upward of 22 533 km^2.

The southernmost Precambrian sandstone area, in the Cree, Athabasca, Black Lakes region, seems to have been free of ice as early as about 9000 years ago. By this time Lake Tyrrell apparently had been drained nearly to the uppermost level of Lake McConnell. If our calculations are tenable, the area south of the proposed south shore of the Lake Athabasca extension of Lake McConnell became exposed through a progressive increase of about 251 m of elevation in about 1440 years. The area between this shore and the south shore of the present Lake Athabasca was exposed much more slowly during the past 8560 years, but probably at a more steady rate than in the preceding 1440 years.

It is probable that the sandy glacial drift south of the present Lake Athabasca was exposed to intense aeolian activity at least until the close of the xerothermic period. The fact that the active dunes are still present suggests that the trees have never been able to stabilize the sand near the shore under the climates that have prevailed since the xerothermic period. It appears that active dune habitats have been continuous in this area for at least 9000 years.

The sandy country east of Great Slave Lake and northward to the arctic coast has had a different history because most of it is in the arctic tundra beyond the limit to which forests have penetrated. It is a broad plain extending northward from the middle Thelon valley to the middle Back River, eastward to uplands north of Baker Lake, northwestward to the Coppermine River, the arctic coast, and around the northeast part of Great Bear Lake. The surface is clothed with very sandy drift like that south of Lake Athabasca and there are thousands of square kilometers of eskers and drumlins composed mainly of sand (Wilson, 1939; Taylor, 1956). Most of the region probably has been free of ice, according to Craig & Fyles (1960), for at least 7000 years, the western parts for perhaps 9000 years (Prest, 1969).

Geologists, archaeologists, surveyors, and casual travelers who have seen this country have mentioned blowing sand, usually forming blowouts or dunes. The tundra has been described as very dry and having scant vegetation in areas not supplied with water by small streams or near the shores of shallow lakes and ponds. A recent visitor to this region, Dr. J. S. Rowe (pers. comm.), reports that there are indeed large active dunes within the Thelon basin, derived from major esker trains.

Our observations in the Athabasca dunes have shown clearly that, in the presence of very strong winds, neither herbaceous nor low woody plants can completely stabilize loose sand, even under the growing conditions of the boreal forest. We suggest that for at least 2000–4000 years the xerothermic climate made a sand desert of the arctic plains, with aeolian activity much greater than it is now. The available descriptions of the

tundra suggest that it would not take a much drier climate to reactivate it. We do not know how much longer the warm–dry period may have been effective in that region. Two periods of warmer and presumably drier climate (2700 to 2200 years B.P. and 2000 to 800 years B.P.), both less severe than the xerothermic period, were proposed by archaeologists in their studies of cultural changes in the vicinity of the treeline (Sorenson *et al.*, 1971).

Physiographic studies in the major sand areas of the Precambrian region are incomplete and thus the total effect of wind is unknown. Large tundra-stabilized dunes have been seen in a few places, but in forested areas they may not appear on aerial photographs. A major effect of wind on the plains north and northwest of the Thelon River may have been on the shape and continuity of the sandy eskers. The elongated ridges south of Lake Athabasca have been greatly altered by wind, and in places converted to isolated hills with rounded forms.

Shore Processes in the Lake Athabasca Sand Dune Region

The history and development of the Lake Athabasca dunes seem inseparable from the shore processes that have been effective during the past 10 000 years as the shorelines of Lakes Tyrrell and McConnell receded northward across a gently sloping plain of sandy glacial drift.

Wind Directions

The most effective wave-producing and sand-moving winds in the Athabasca dune region now come off the lake from the northeast or from the westerly quadrants. The directions of prevailing and storm winds in the Mackenzie basin during the last 10 000–14 000 years are speculative but it is clear that there have been major changes. David (1981, see above) applies to all of the Mackenzie basin his explanation that there was a change from dune-forming southeasterly winds in the Cree Lake region to the later ones from the northwest which came after about 8800 B.P. If this and our own estimates for lake chronology are approximately correct, the shore processes described below would have become effective about the time Lake McConnell was formed. When this happened, on the southern shores of Lake McConnell, the west, northwest, and northeast winds would have blown unimpeded a much greater distance across open water than they do on the present shores. From the northeast the distance was only about a third larger, but for westerly winds it was seven to eight times as great. For perhaps 4000–5000 years the winds when over the land, whether from the southeast, northeast, or west, were mostly unobstructed by forests.

Wave Action

The period in which wave action is possible is strictly limited to the ice-free period, which on Lake Athabasca usually lasts from about mid-May to sometime in October. The most effective winds during this season come with violent storms. Winds from the northeast are usually accompanied by a certain amount of rain. These storms appear to be cyclonic and are followed by usually dry northwest and west winds of nearly equal force. Occasional winds of gale force also come from the southwest and, though they may continue unabated for three or four days, they are infrequent. Although these winds may not have direct effects upon the south shore, they may temporarily alter the water level in the eastern part of the lake and, thus, affect the strand lines.

Points of land jutting into the lake affect the disposition of sand and other sediments. Some sand apparently goes into off-shore bars, which are clearly visible in certain aerial photographs (Figure 9). Smith (1978) counted 23 bars in the shoals near William Point. Some of the sand is carried along the shore to form shoals off points of land and in bays with lee shores behind the points. These effects are seen at William, Beaver, and Wolverine Points on the south shore and also at the mouth of MacFarlane River. The nearly symmetrical distribution of shoals off the points suggests that winds from the northeast and northwest are equally effective in moving the shore sands.

Ice Push

On the shores of the large northern lakes ice push is due to the movement of windblown masses of ice over the surface of the lakes (Tyrrell, 1909; see also Scott, 1926, for a general discussion of ice push). As the ice melts in the spring it disappears first from the shores, leaving lanes of open water surrounding central bodies of floating ice. The

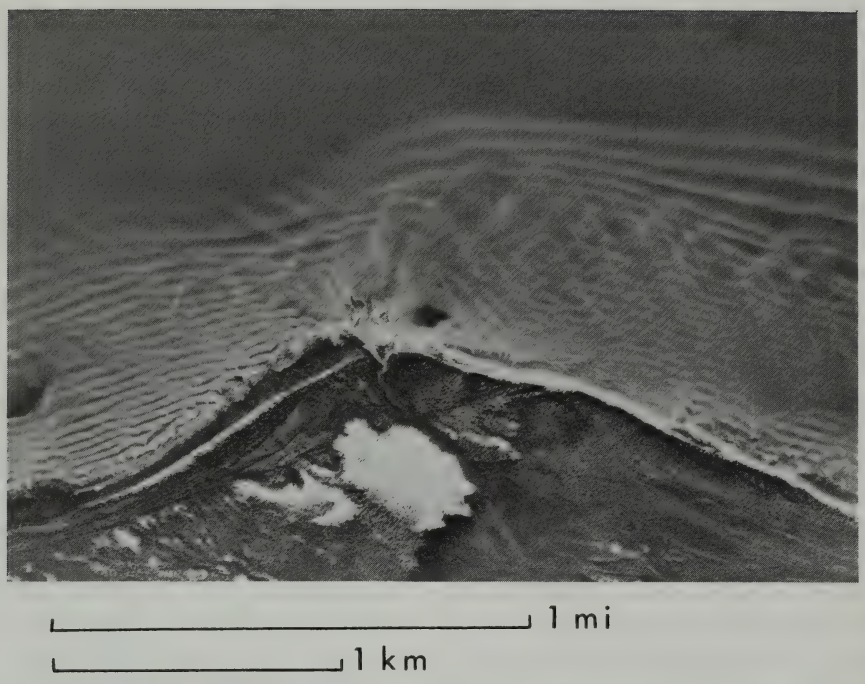


Figure 9. Vertical aerial photograph of the offshore bars deposited around a small point of land between Wolverine Point and the MacFarlane River. (Sask. Dept. Tourism and Renewable Res. photograph YC 7624-64.)

Figure 10. Ice push ridge at Poplar Point composed of sandstone slabs. The trees on the ridge are *Pinus banksiana, Betula neolalaskana, B. occidentalis*, and *B.* × *winteri*.

remaining ice mass can be moved by ordinary and storm winds. When an ice mass hits a shore it drives shore materials into ridges or greatly modifies any ridges already there. Great boulders are often forced inland for many meters and sometimes plow a trench as they are shoved along. The ridges of heavy sandstone slabs near Poplar Point (Figure 10) probably were pushed up by ice.

Beaches

Existing sand beaches are unstable due to wind, wave, and ice action and to fluctuation in lake levels over periods of time that are within the life spans of any plants that might stabilize the sand (see Stockton & Fritts, 1973; Raup, 1975). The sand is worked into small dunes and ridges, often subtended by small lagoons, and temporarily stabilized here and there by scattered herbaceous perennials and a few shrubs (Figure 11). Some of these plants also are common on the large inland dunes.

Shore Ridges

Immediately back of the present beaches is a series of raised "fossil beaches," all but the lowest of which have long been protected from wave and ice action. In a few places, such as at Turnor Point, they are of gravel, but most are of sand. They range in height to 35 m or more above the lake and are separated by long narrow lagoons or by dry intervales. They have become partly stabilized by dune grasses, shrubs, and/or by *Picea glauca* var. *albertiana* (Figures 7 & 11). The stabilization is not complete, for the sand is dry and easily blown out by the wind. The tops of the ridges acquire a "grooved" appearance, and the direction of the grooves depends upon the angle between the trend of the ridge and the direction of the wind. Northwest winds on this shore produce diagonally-orientated blowouts on most of the ridges. Elongated ridges farther from shore also show the same process. These blowouts can be seen in all stages of development. Many ridges are thus reduced to

Figure 11. Beach and sand ridge at Thomson Bay. The pond near the lake edge is filled with *Carex aquatilis* ; on a beach dune behind it is a thicket of *Salix planifolia* ssp. *planifolia* and ssp. *tyrrellii* and *Myrica gale*; the the sand ridge is partly stabilized by *Picea glauca* var. *albertiana* forest.

series of dune-like hills, with dune slipfaces on the lee fronts. Sand blown out of the ridges immediately falls into the intervales between them and, depending upon the thickness of the ridge sand and the space available, parabolic dunes are formed. In general, the ridges are more or less parallel to the present shore but exceptions occur on projections of land, such as William Point, or among ancient beach ridge systems far back from the present shores.

The origin and development of the high shore ridges require further study. Hermesh (1972) treated them as dunes, perhaps as "foredunes" in the sense of Cooper (1958) and others. It is more likely that they originated as offshore bars modified by wave action and ice push as isostatic rebound brought them above lake level where they could be partly stabilized by vegetation and modified by wind. Smith (1978) dug pits on a high shore ridge near Ennuyeuse Creek and found many coarse inclusions in its sand. He suggested that lake ice either brought them from other shores or dredged up offshore stones and deposited them in an ice push ridge.

River Deltas

The largest streams flowing into the lake between the Athabasca and Stone Rivers are the William and the MacFarlane. The William River has built a delta that extends about 13 km into the lake and is about 13 km wide at the base (Figure 12). The position of this delta on the shore of the lake is conducive to maximum movement of the sand by waves and wind, for it is on the northward bulge of the south shore where there are wide stretches of open lake to the northwest and the northeast. The MacFarlane River delta, on the other hand, is near

Figure 12. Oblique aerial view of the William River delta showing a series of old, partly stabilized beach ridges. The Thomson Bay dune field appears in the upper right. (National Air Photo Library photograph A 2595-5.)

the beginning of a northward trend of the lake shore, so that northeasterly storm winds are not as effective as at William Point. The MacFarlane may deliver less sand to the lake than does William River, though we have no data to support this.

Plant Habitats in Regions of Actively Blowing Sand

Our primary interest in the Lake Athabasca sand dune area is botanical—its flora and vegetation — and our object here is to describe the plant habitats and the vegetation of the region. The habitats available for plant life vary from dry sand, continuously blown about by the wind, to relatively stable soils and surfaces with moisture regimes from dry to wet.

Two hundred and sixty-six kinds of vascular plants have been found in the area, about 80 percent of which are characteristic of and more or less wide-ranging in the boreal coniferous forest region. The remaining 20 percent come from northern grasslands, arctic tundra, or the northern cordillera. About 40 of them are so constituted by low moisture requirements, growth habits, and tolerance of abrasion and burial by aeolian sand, that they can live on the open dunes. At the other extreme is a much larger number tht are restricted to wetlands such as muskegs and lake shores. Between the extremes are many plants that have varying tolerances on both the moisture and physical disturbance gradients. Local differences in the temperature patterns probably have little effect upon plant distribution in the region.

Some major factors influencing the habitats of the region are: (1) relatively low precipitation, a short growing season, and frequent high winds; (2) sandy soils derived from glacial tills that have been progressively reworked by shore processes and wind on the receding strandlines of postglacial lakes; (3) fire that, by maintaining a degree of instability in the forest vegetation, has favored fire-adapted species; and (4) wetlands that have been produced by a relatively high water table and the alteration of drainage systems by the deposition and deflation of aeolian sand.

The active sand dunes present a varied and biologically demanding set of environmental conditions for plant growth. For these reasons it is important for us to define the different kinds of aeolian depositional and erosional features in the area so that these features can be discussed in relation to the vegetation.

Dunes and Dune-forming Processes

Sand dunes result from the interaction of sand, wind, and water. Wave action sorts shore materials and delivers sand to beaches where it can be blown by wind. On the south shores of Lakes Tyrrell, McConnell, and Athabasca sand has been abundant, and the rising land surface has brought the beach sands up into the winds more rapidly than otherwise would have been the case. Ice push has furthered this process. Diversity and irregularity in the resulting land forms are due to their positions with respect to prevailing winds, to vegetation, and to frequent fires that have affected the control of the sand by the vegetation.

An examination of the sand dune areas on aerial photographs (and by flying over them) reveals a bewildering array of forms, ground plans, and orientations. Our attempts to fit them into the few standard categories described in the literature have not been completely satisfactory. Smith (1978) was probably correct in thinking that much of the difficulty in dune classification is due to the wide range of variation in effective winds (see below). It is probable that the dune forms and orientations in the area will not be rationalized until adequate data on the direction, intensities, and seasonality of these winds have been accumulated. Their general effectiveness rests upon the nearness of the dune areas to the open lake and upon the prevailingly dry climate of the region.

We have no data on precipitation in the dune areas but extrapolation from Uranium City and Chipewyan records suggests that the total for the year averages 36–40 cm. About 25 of this comes as rain, roughly half of it in the growing season (June, July, and August). Rain seems to have only a temporary effect on the movement of dune sand. In making moisture profile measurements two days after about three days of heavy rain Hermesh (1972) wrote, "The surface 5 cm were dry and blowing." The winter snow is relatively dry and powdery and gets mixed with blowing sand. A trapper near Ennuyeuse Creek told us that winter travel on the dunes with sleds was impossible because the sleds would not run on this mixture. As yet we have no way of evaluating the movement of sand by the winter winds.

In view of the above-mentioned deficiencies in our knowlege of factors governing the geography

of the dune areas, and in view of our major purpose, which is the delineation of the history and present condition of plant habitats in the dunes, we are constrained from attempting a thorough classification of the dune forms. These forms are of less significance for our purpose than the general prevalence of windblown sand. In order to facilitate the discussion of vegetation, however, we will describe some of the most conspicuous aeolian depositional and residual forms. In doing this, we will attempt to avoid genetic classifications that imply more than we know about the origin of the features and we will treat the multitude of forms mainly on a descriptive level. The outline of our presentation is as follows: *aeolian depositional features:* parabolic dunes, oblique ridge dunes, transverse dunes, precipitation ridges, and other dune features (sand hillocks, sand sheets, and rolling dune topography); *aeolian residual features:* gravel pavements and dune slacks.

The Sand Supply

The sand supply for the Lake Athabasca sand dunes is ultimately provided by the Athabasca Sandstone that underlies the region and from which sandy glaciofluvial materials were derived. As the lake levels of Lakes Tyrrell, McConnell, and Athabasca dropped through drainage and as the land level rose by isostatic readjustment, the glaciofluvial materials were worked by water and ice action and lacustrine deposits were exposed to the wind along the south shores of these lakes. At the same time, the major streams from the interior, the William and MacFarlane Rivers, which today mark the major dune fields, carried large quantities of sand into the lakes.

The large dune fields are actively enlarging on their eastern and southern perimeters, more rapidly on the former than the latter, and in some places even on their western edges (Figures 54 & 56). In only a few places do the dunes come out to the lake edge (Figure 58). In most places a series of plant covered and semistabilized ridges and hollows separates the dune fields from the lake and a supply of new sand. It is probable that the amount of new sand being delivered to the active dune fields has diminished (David, pers. comm.) and some evidence of sand starvation has been observed. Isostatic readjustment is still continuing, as shown by series of uniformly spaced offshore bars (Figure 9) that occur in many places along the shore. However, the rate of rise is probably less than it was in the past. Noble (pers. comm.) using ^{14}C dates on successively lower beaches around the eastern part of Great Slave Lake, concluded that isostatic adjustment was still active, though progressively slower during the last 2000 years.

If our concept of the northward advance of trees is acceptable, a gallery forest of Alberta white spruce probably had reached the shores of Lake McConnell via the William River at least as early as 8500 years ago. Pines may not have reached the shore area until the close of the xerothermic period, perhaps 5000 or 4000 years ago. The present pattern of shore ridges, dune fields, and forests probably has been duplicated repeatedly during this time, not in exact detail but in general outline, and the function of the white spruce as a partial stabilizer of the sand probably has been effective for 4000–5000 years longer. Under these circumstances, and assuming that the isostatic rebound still continues, the stabilization process that we see going on now may well be transient.

The apparent stabilization of sand along the shore and among the dune fields becomes still less impressive when the effects of fire are considered. All of the forests that border the large fields are extremely susceptible to fire and have been burned repeatedly. The fires have been started by lightning or from the campfires of the Indians who probably have inhabited the region as long or longer than it was forested.

Forest fires within 15–25 km of the lake shore expose the sand to the winds and initiate blowouts, of which there are a great many current examples. Most of them start as small parabolic dunes and those farthest from the lake may continue and enlarge as such to the proportions of the ones seen near Archibald Lake and in the Maybelle River area. There is some evidence that the smaller dune fields such as those on both sides of Wolverine Point started from fire-induced blowouts.

Aeolian Depositional Features

Parabolic Dunes

The most common dunes in the forested region south of Lake Athabasca and on the forested borders of the large dune fields are parabolic in plan view with tails pointing to the windward and a convex face on the downwind side. Parabolic dunes appear as both active and inactive (paleo-

dunes) features. They were equally common in the past, to judge from the large number of stabilized border ridges and associated patterns that traverse the landscape.

Cooper (1958) described parabolic dunes formed by the rejuvenation of partly or wholly plant covered sand dunes. Changes in climate, wind direction, or more commonly fire, may initiate breaks in the vegetation cover leading to the formation of blowouts and the reactivation of the sand. Blowouts may take the form of saucers or troughs (Figure 13). *Saucer blowouts* are small and often short lived unless they merge with other such forms; then the possibility of their developing into parabolic dunes is greater. *Trough blowouts* are large and trough-shaped and characteristically lead to parabolic dunes. According to Cooper (1958, p. 74) "Three conditions are necessary for initiation of a trough blowout and its development into a parabolic dune: (1) considerable thickness of sand, (2) a surface stabilized by vegetation, but with points of weakness, and (3) essentially unidirectional effective wind."

Parabolic dunes may exist in a number of forms (David, 1977). They may be symmetrical, asymmetrical, filled, or partly filled. Their tails, which are produced by the lateral scattering of sand as the dune advances, may be traced for long distances. These parallel ridges were described by Hack (1941) as "longitudinal dunes." The concept of the longitudinal dune as one originating from a parabolic dune that has broken through its advancing head has also been proposed by Verstappen (1968) and by Cooke & Warren (1973). The "Cree Lake type" recently discussed by David (1981) are considered by him to develop as parabolic dunes. Such longitudinal dunes would have been formed by a unidirectional wind and would not fit Cooper's multidirectional wind hypothesis (1958) or other views on the origin of longitudinal dunes as summarized by Mabbutt (1977). Because of the confusion that would be introduced by using the

Figure 13. Trough blowout cutting through a jack pine forest northeast of Little Gull Lake. The trough is narrow and about 9 m deep. Its gentle, peripheral slopes are being stabilized by *Hudsonia tomentosa* along with *Calamagrostis, Festuca, Deschampsia,* and *Tanacetum.*

term longitudinal dune or longitudinal ridge for the tails of a parabolic dune we will here use the term border ridge (David, 1977).

North and east of Archibald Lake the upwind "tracks" of the active parabolic dunes show evidence of many lesser blowouts and parabolic dunes that are still active enough to appear on the aerial photographs. Seen from the air, they make a curious lace-like pattern which appears to be the "embroidery" pattern described by David (1977). This pattern covers many square kilometers in the Archibald Lake area (Figure 57) though active parabolic dune fronts may be absent. Something like it also is shown in Figure 14 where it occupies long "corridors" between the prominent east-west ridges that have been interpreted as elongated drumlinoid features (the "ispatinows" of Tyrrell & Dowling, 1897).

The variation in size and area of parabolic dunes is great. North of Archibald Lake four small parabolic dunes are coalescing and moving into the lake (Figure 57). The largest of these dunes is 1.2 km long and 0.4 km wide. The original parabolic dunes that made up this complex are still distinct and their border ridges can be traced to the northwest. The dune complex west of the Maybelle River is also the product of the coalescence of two or more large parabolic dunes. This dune complex covers about 25 km^2 and has formed a dune field that supports a large series of transverse dunes (Figure 53). Border ridges which trace the movement of these dunes from the northwest are still visible. The Wolverine Point dune fields appear to be still larger parabolic dune complexes which have formed by the confluence of several individual dunes. The dune tracks and

Figure 14. Oblique aerial view of the Lake Athabasca shore between Wolverine Point and the MacFarlane River. The foreground pattern of stabilized border ridges and precipitation ridges is the embroidery" pattern referred to by David (1977). The MacFarlane River dune field appears in the upper right. (National Air Photo Library photograph A 2595-66.)

the inland border ridges are visible on aerial photographs.

David (1977) would derive all of the dune fields south of Lake Athabasca from parabolic dunes and there is some evidence to support this view. The northern edge of the MacFarlane River dune field (Figure 59) shows a series of parabolic dunes separated by narrow bands of forest forming a series of "in succession parabola dunes" (David, 1977). In the main dune field south of the "in succession" dunes, however, evidence of the possible origin of the dune field from parabolic dunes is obscure. The origin of the William River dune fields is even less clear and it could be concluded from the evidence that this and other large fields have always existed as we see them today.

Two methods were used to determine the rate of movement of a parabolic dune complex at the eastern margin of the Wolverine Point dunes. The first method was applied to a small pine less than 40 years old that was partly buried by an advancing dune front and whose completely covered lower branches were dead (Figure 15). The age of the tree at the uppermost of the dead branches was subtracted from total age. The distance from the base of the tree to the edge of the dune front was measured and an advance of about 50 cm in the preceding five years was obtained. A second method was used where the slope of the dune front and the height of the front were much less. The growth rings in small trees growing in the open are nearly circular and concentric. When sand begins to cover a tree and to press upon its stem, compression wood develops on the side opposite that on which the pressure is applied. Thus the growth rings become oval and eccentric. By counting the number of years since this eccentric growth began in a tree about 40 years old emerging from a dune front about 1.5 m from the edge of the front, it was estimated that a 1.5 m advance had occurred in the preceding five to ten years. The

Figure 15. Precipitation ridge at the margin of the Wolverine Point dune field invading a *Pinus banksiana* forest.

first method of calculation gave a rate of advance of 10 cm per year, and the second method gave a rate of 15–30 cm per year.

Oblique Ridge Dunes

In the large dune fields at the William River there occur the most massive and conspicuous dunes in the Lake Athabasca region (Figures 16 & 17). These dunes have a shallow parabolic shape in plan view, convex to the northeast (Figure 19). About 40 of them form a band through the center third of the field west of the William River and several occur east of the river, the former trending in a northwest - southeast direction (Figure 54). Hermesh (1972) gave the orientation of these dunes as N32 – 41°W in the northern part and N53 – 61°W in the southern part. The larger dunes vary in length from 0.5 km or less to about 1.5 km. They are free-standing on a broad plain-like surface that slopes gently to the north. This surface is flat to gently rolling and most of it is covered with a gravel pavement on which there are occasional sand lenses or hillocks. Some of these dunes rise more than 35 m above their base but others, particularly in the southeastern part of the area, are low and indistinct. Their crests are sometimes rounded (Figure 18) but most have slip faces on the southeast side or on both sides with a "knife-edge" crest between (Figure 17).

In profile one of the higher dunes with a "knife-edge" crest had steep eastern and western slopes, the former being slightly steeper. Below the crest the steep easterly slipface bellies out and is rounded convex to the base. The western slope presents a smooth unbroken profile becoming progressively less steep toward its base. A windrow of organic debris, probably moved by a recent strong westerly wind, was located about two-thirds of the way up the western slope of the dune.

Some oblique ridge dunes have prominent peaks and cols, sometimes as many as three (Figure 38). On the western side of the dunes there may be a ridge located behind each peak (Figure 18). These ridges may be formed by the channeling of wind around the peaks of the dunes,

Figure 16. Aerial view of an oblique ridge dune moving across a gravel pavement plain in the William River dune field. This northwesterly view shows the lee slope of the dune which is partly covered by herbaceous flora (cf. Figure 38); Lake Athabasca appears in the distance.

Figure 17. Oblique ridge dunes characteristically have a knife-edge crest. A series of other oblique ridge dunes and Lake Athabasca appear in the distance. (Photograph by R. Hermesh.)

Figure 18. The gently curved windward slope of an oblique ridge dune looking toward the south southwest. Sand ridges sometimes join the main the dune at right angles.

the lateral erosion of the windward sides of the dunes, and deposition behind the peaks. Tapering tongues of sand appear at the ends of the dunes. These usually point southwestward, but some are directed northeastward as well. New sand available to these dunes seems to be limited to what can be winnowed from the sandy-gravel till overlain by gravel pavement on which the dunes sit and from the surrounding sand hillocks and sheets.

Oblique ridge dunes in the William River area are strongly influenced by winds from more than one direction. Local meteorological data are not available for the area but our field parties have experienced very strong winds from the northeast, northwest, west, and southwest and we have seen some small dunes orientated to southeasterly winds. At the western end of Lake Athabasca, gale winds from the southwest were experienced in August, 1930. Late in July of 1935, there was a four-day gale from the northwest followed by two days of very strong northeasterly winds; in August there was a series of gales or very strong winds from the southwest (2), northwest (6), and northeast (2). On 16 August 1935, a strong northwesterly wind was blowing "clouds" of sand, clearly visible at a distance, off the western slipfaces of the large oblique dunes and distributing it on the eastern slopes of the knife-edged ridges. There is also botanical evidence to suggest that westerly winds are predominant during the growing season. On oblique ridge dunes herbaceous vegetation occurs only on the east side of the base of the dunes. In order for seedlings to become established they must be located where sand is accumulating slowly and where the surface is not eroding (see below). This condition would prevail on the east side of the dunes only if westerly winds were predominant.

The action of contrary winds on oblique ridge dunes may have slowed their easterly movement, if it has not actually stopped it. A comparison of aerial photographs taken in 1957 and in 1976 (Figure 19) shows no appreciable change in form or position in the oblique ridge dunes. Using our figures for the rate of advance of precipitation ridges and transverse dunes their movement could not have been more than 12 m during the 19 years between photographs, and would not be discernable on the photographs. But the photographs do show that vegetation has expanded during that time both at the northern edge of the dune field and in the lee of dunes. This may indicate a slowing in the rate of sand movement.

The name for the high dunes, which we call oblique ridge dunes, has been a persistent source of confusion. Hermesh (1972, p. 122) termed them "longitudinal dunes" and commented that "successive dunes are often aligned along the same axis forming dune chains." The aerial photographs (e.g., Figure 54) suggest that some of them are rather roughly aligned from northwest to southeast; but the longest continuous group is only about 1.6 km long, no longer than the largest single dune. Those that seem to be in rough alignment are commonly more than 0.8 km out of line. It is doubtful that the "chains" are any more than a suggestion of continuity. Rowe & Hermesh (1974) called them "seif dunes" but David (1977) stated that this term should not be used because seifs are straight continuous ridges that extend over long distances. Smith (1978) called them "transverse dunes" apparently following David (1977), who suggested at that time that they may be the same as this more unstable, shorter-term dune form which may be affected readily by winds of varying directions. If they are formed by winds from two directions only, they would be orientated to the resultant of these winds. Cooper (1958) termed such dunes "oblique ridge dunes" and we feel that his concept best fits the high dunes in the Lake Athabasca area. David (pers. comm.) claims that the name "open parabola dune" should be applied to them because of their shallowly parabolic shape in plan view and because of a lack of information on the wind directions that control these dunes. We have decided that there is sufficient evidence that these dunes are influenced by winds of more than one direction, at least during the summer, to justify using Cooper's name – oblique ridge dunes.

Transverse Dunes

Transverse dunes are orientated at right angles to the direction of the effective wind and concave to windward. The lee slopes are slipfaces that are as steep as the sand will hold, usually averaging 33°. The slipface may extend to the top of the ridge but more often the upper edge breaks from a gently rounded upper surface which is confluent with the upper windward slope at the top of the ridge (Figure 20). In some places, even in the absence of vegetation, the slipface may be absent and the lee slope is gentle from top to bottom (Cooper, 1958).

Authentic free-standing transverse dunes in the central parts of the large dune fields appear to be

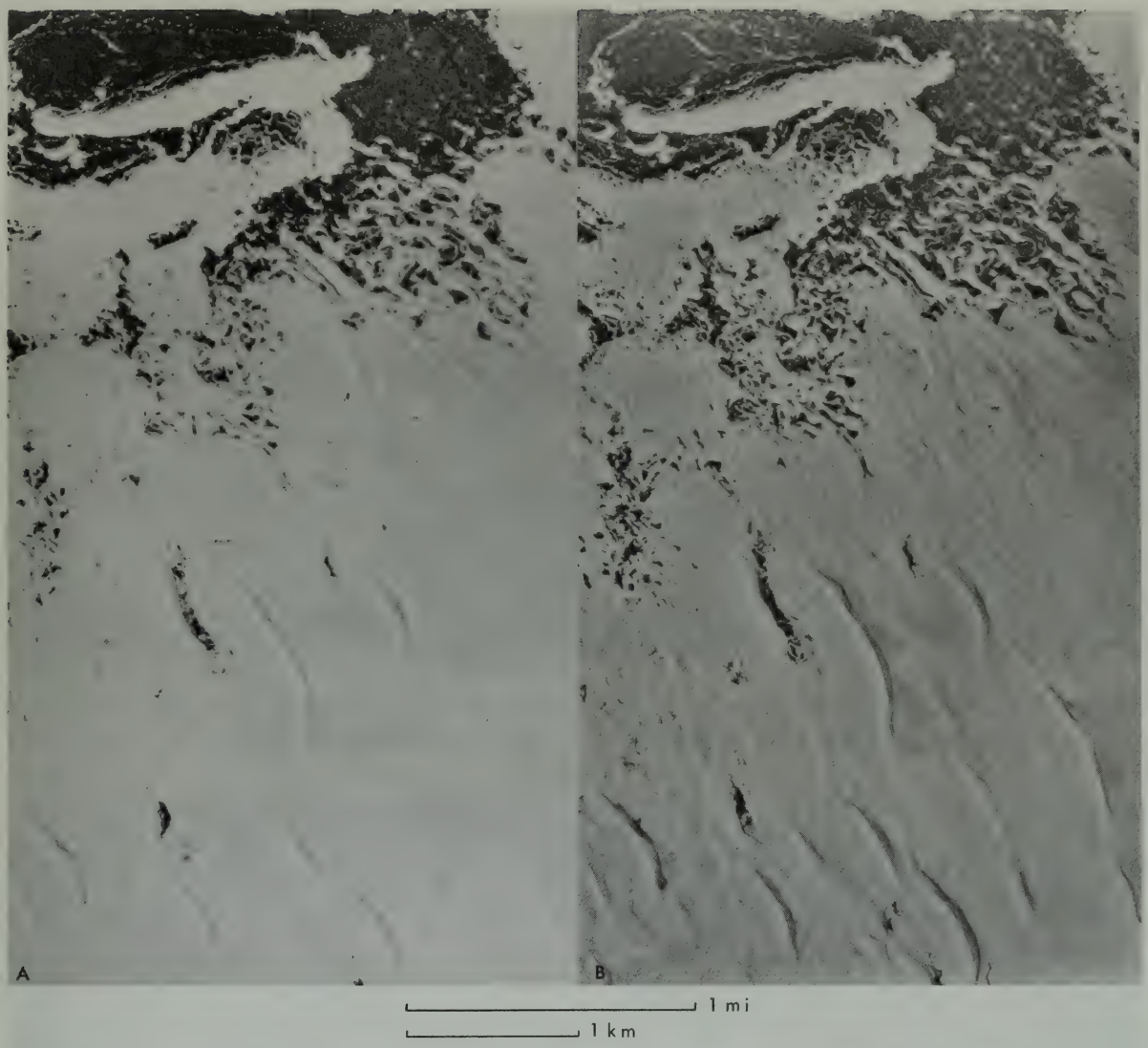


Figure 19. Vertical aerial photographs comparing oblique ridge dunes and patches of vegetation at the northern edge of the William River dune field. Photograph A was taken in 1957 and enlarged to the same scale as B taken in 1976. There is no evident change in the shape or position of the oblique ridge dunes during the 19 year period. A conspicuous change is visible, however, in the development of vegetation during that time within the dune field and at its borders. (A. National Air Photo Library photograph A 15611-9; B. Sask. Dept. Tourism and Renewable Res. photograph YC 7624-18.)

rare because most of the effective winds in these fields are not unidirectional. Those we have seen are in localities where the northeasterly winds are relatively ineffective due to obstructions formed by forests or points of land. Most of those mapped by Hermesh (1972) are in the northwest part of the Thomson Bay field where they are more or less protected from northeasterly winds by Beaver Point, and in the northern part of the William River field where William Point has the same effect. Hermesh gives the orientation of those he identified as 312°–025°, indicating that they were being moved by westerly winds varying from west northwest to southwest. Transverse dunes also occur as large fields in the parabolic dune complexes such as the Maybelle River dunes (Figure 53) and the Wolverine Point dune field (Figure 58).

Figure 20. A transverse dune invading a dry dune slack in the Wolverine Point dune field.

Figure 21. Blowing sand drifting across a "willow dune" in the Thomson Bay dune field. *Salix silicicola* appears in the foreground and *S. planifolia* ssp. *tyrrellii* in the distance.

The rate of movement of transverse dunes was calculated by Hermesh (1972) by excavating plants of *Tanacetum huronense* var. *floccosum*, measuring their annual growth, and using a lee slope angle of 30–32°. He estimated that between 1967 and 1971 one of the dunes he measured advanced 36–70 cm per year and a second dune advanced 25 cm per year.

The importance of vegetation to the formation of transverse dunes is a subject of controversy. Cooper (1958) stated that wherever unidirectional wind is acting upon a heavy accumulation of sand unencumbered by vegetation transverse dunes will be formed. Other authors have argued that vegetation is essential for maintenance of transverse dunes because this type of dune is essentially unstable and, without stabilization, will be converted into barchan or longitudinal dunes (Enquist, 1932; Bagnold, 1941). Their argument may be valid where the supply of sand is small but, where the supply of sand is great, transverse dunes are distinct and can maintain their individuality as they move forward.

Hermesh (1972) recognized two kinds of transverse dunes of the freely moving type based on their dominant vegetation. He called those that reach heights of about 12 m "birch dunes" (Figure 33) and 3–6 m high "willow dunes" (Figure 21). He thought that the different forms and growth habits of these plants were responsible for the forms and sizes of the dunes. The sparse vegetation we have seen on them, however, shows little stabilizing influence. At most, it may modify a dune's shape by giving it a more gentle crest and a less pronounced slipface. Transverse dunes may be formed, in fact, in the absence of vegetation (Cooper, 1958). We prefer, therefore, to consider the willow and birch dunes merely as parts of a continuum of variation among dunes and their vegetation.

Precipitation Ridges

Prominent on the perimeters of the large dune fields is a dune form that Cooper (1958) has referred to as a precipitation ridge. When a moving dune meets vegetation, the velocity of the wind is reduced and the sand piles up to form a ridge with a leeward slipface. In general, the ridge will be about as high as the vegetation is tall. Vegetation is not essential, however, for the formation of a precipitation ridge. Such ridges occur where a dune field is moving into a lake, river, or marsh vegetation as well as where forest is encountered. Given sufficient sand and wind, the ridge continues to advance, its slipface inundating and burying the vegetation. The best defined and most conspicuous precipitation ridges are, of course, those invading forests (Figure 15). They reach heights of at least 12 m above the floor of the invaded woodland.

At the inland perimeter of all of the larger dune fields, but most conspicuous on the eastern and southern sides, there are active precipitation ridges. Old, stabilized precipitation ridges occur occasionally just outside the present areas of active dunes (Figure 59), but long continuous ridges are not known any distance south of the large fields. This suggests that these active dune fields may not have extended further inland than they do at the present time or that their old precipitation ridges have been reworked and obscured by parabolic dunes.

Aerial photographs usually show the margins of the dune fields invading forest as relatively sharp lines. In detail, however, the lines are somewhat scalloped, with slipfaces usually convex to leeward, but sometimes concave, particularly where a stream or river is eroding the front. The forward convex bulges have led David (1977) to suggest that they are really the advancing fronts of parabolic dunes, but it seems to us that the variation from convex to concave could as easily be accounted for by the prevailing variation in the heights of vegetation being invaded.

Other Sand Features

Not as prominent as the oblique ridge and transverse dunes, but perhaps more important in terms of their areal extent, are the sand hillocks, sand sheets, and rolling dune topography. Some of these features may be early stages of oblique and transverse dunes, but most may pass through a cycle of aggradation and degradation without assuming an easily characterizable dune form.

Sand Hillocks. Small sand accumulations, seldom over 0.6–1 m high, that form around or in the lee of small obstructions such as large cobbles, boulders, individual plants, or small groups of plants, are called sand hillocks. In the absence of these obstructions they are sometimes found as low lens- or shield-shaped dunes. In ground plan they may be more or less streamlined with narrowing "tails" or "tongues" extending downwind (Figure 22), or nearly circular and shallowly dome-shaped. Terms used for them in the literature are "tongue," "cushion," "microdune," or

Figure 22. Hillock dunes in a dune slack in the Maybelle River sand dunes. Winds blow through the trough-like slack and build up small dunes in the lee of clumps of *Hudsonia tomentosa* and grasses.

Figure 23. Area of rolling dunes in the William River dune field.

"minor" dune. Hermesh (1972) used "minor" dunes for the ones he saw in our area, while Smith (1978) called them "phytogenic" dunes. Though most of those seen in the Athabasca area are phytogenic, many are formed by other small obstructions or they may appear as shallow lens-shaped mounds without any obvious obstructions. Another term, "embryonic dune," is sometimes used, but this implies that they are the beginning stages in the development of larger dunes, which may or may not be the case. In the large dune fields, where there is an abundance of blowing sand, they are most likely to be ephemeral. In marginal situations they may be early, though possibly ephemeral, stages of stabilization.

Sand Sheets. As the term implies, these are merely thin covers of sand distributed more or less evenly over flat-lying or gently sloping surfaces; usually on gravel pavements (Figure 45). They are common in the central parts of the large dune fields.

Rolling Dune Topography. Hermesh (1972) described and mapped large areas of what he called "rolling dunes" (Figure 23). The largest areas are in the eastern and southeastern parts of the William River field, in approximately the eastern half of the Thomson Bay field, and south of Yakow Lake in the MacFarlane River dunes. Lesser areas are south of Beaver and Wolverine Points. His description was as follows: "These dunes form a gently rolling landscape devoid of shrubs or trees. Their height ranges from 0.5 to 12 m. Mature dunes are up to 750 m long and 75 m across. Crests are rounded, forming broad, almost flat tops. The slopes are never steeper than 10-12° " (Hermesh, 1972, p. 115). And " . . . they form a series of parallel oblong ridges, the long axis of which was aligned N35–44° W among the dunes near the William River, and between N40–60° W among the Yakow Lake dunes. The alignments coincide with those of the longitudinal and transverse dune in the same areas" (Hermesh, 1972, pp. 118-119).

Hermesh stated that these dunes formed a genetic sequence leading to the large oblique ridge dunes in the William River field. He described them in four types according to size, from heights of 0.5 m up to about 12 m, and also according to the density of their herbaceous vegetation, which he believed determined their form. He thought this vegetation was responsible for their rounded tops and gentle slopes. He noted that on the higher dunes slipfaces were formed, presumably because the gradually thinning vegetation was less effective there. He stated "There is no abrupt change between the rolling and longitudinal dunes. All gradations from low rolling to large longitudinal dunes are found. Fifteen to twenty m high dunes of an intermediate type commonly occur as isolated examples among fields of lower rolling dunes" (Hermesh, 1972, p. 126).

In the Yakow Lake area Hermesh associated rolling dunes with the transverse type. In this area they have alignments paralleling this type and have a "distinctly steeper east slope" (Hermesh, 1972, p. 119). On the same page he associated them also with precipitation ridges, saying that they often form behind the latter as they advance over forests. In the small dune areas at Wolverine Point he mapped only rolling dunes, though we found well-formed transverse dunes there, with steep slipfaces.

His rolling dunes are indeed abundant where he mapped them in the William River and Thomson Bay fields. His analysis rests heavily upon their being truly phytogenic and on the assumption that all or nearly all of their plants germinated in damp to wet sand in dune slacks and then grew up through the sand as the latter accumulated to form the dunes. However, we have found some taxa that clearly had germinated far above the slacks, and appeared to have had only ephemeral effects on the sand movement. Further, we have seen one or another of the dune willows on the rolling dunes. Some of the high oblique ridge dunes have rounded tops in the complete absence of vegetation and some of the lower rolling dunes show incipient slipfaces.

It has already been pointed out that the high dunes in the William River field probably owe their form and orientation to the interplay of northeastly and westerly winds. We suggest that the rolling dunes may be formed by the same opposing winds, which are here less effective and may be orientated in various directions.

Smith (1978, p. 42) used Hermesh's term, "rolling dunes," as a catch-all for the, "vast area of the dune fields which lack dunes of classical or distinctive shape." David (1977), who studied the Athabasca dunes only from aerial photographs, seems to have sensed this confusion of forms. He sought to rationalize it by a combination of the formation of parabolic dunes and an associated "embroidery" pattern.

With our present knowledge of the dune forms and of the winds that produce them we are unable

Figure 24. A gravel pavement ridge in the William River dune field. The sun is reflecting off the polished faces of the ventifacts that form the gravel pavement.

Figure 25. View north across a barren plain covered with gravel pavement in the William River dune field. Oblique ridge dunes appear on the left and in the distance.

Figure 26. Ridge of unsorted boulders, gravel, and sand near the southern edge of the Thomson Bay dune field just east of Little Gull Lake.

to confirm or deny Hermesh's or David's analyses of these dunes. We use the term "rolling dune" as Smith used it as a catch-all for a multiplicity of forms which present essentially the same habitat for plants – that of active windblown sand.

Aeolian Residual Features

Gravel Pavements

The deflation of material containing gravels too large to be moved by wind leads to the formation of a lag deposit that we are calling gravel pavement (Figures 24 & 25). Other terms have been applied to this feature: desert pavement (Bagnold, 1941), gravel plain (Holm, 1960), and pebble covered deflation surfaces (Smith, 1978). Since our area is neither a true desert nor always a plain, and since Smith's expression is cumbersome, we are using the term gravel pavement.

In the Lake Athabasca area, gravel pavements typically consist of a single layer of gravel over sand that may or may not contain coarser grains and scattered gravel. In some pavements the layer of gravel is up to two to five cm deep, and in others it may consist of a range of coarse materials from pebbles and cobbles up to boulders one meter in diameter. This diversity in pavement surfaces is related to the origin of the coarse materials which can be traced to (1) glacial and fluvial deposits that were reworked by water in postglacial Lake McConnell and later by wind, and to (2) unmodified glacial deposits that have been worked by wind into a lag concentrate.

On the present shore of Lake Athabasca there is much variation in gravel beaches, but all of those that we have examined consist of a layer of gravel more than one stone thick. It is possible that some of the pavements with a deep layer of gravel overlying sand originated as a beach deposit, but it is unlikely that pavements with a single layer of stones originated in this way.

In most gravel pavements the distribution of gravel on the surface is more compatible with the action of wind and gravity than with lake action. A transect across a gravel pavement ridge near Little Gull Lake showed a crest with a mixture of sand

Figure 27. Polished and faceted ventifacts on a gravel pavement.

and gravel to a depth of 10 cm overlying sand that contained occasional pebbles. From just below the crest of the ridge to the foot of the slope the pavement covered sand that lacked coarse inclusions. It is assumed that the crest represented glacial till that was worked by wind to yield a lag concentrate. Some of the coarse materials were moved downslope through the action of wind and gravity, probably assisted by frost action, to their present position overlying pure sand. The ability of wind to move gravel was shown in several places where pebbles up to 3 cm in diameter were overlying moss mats or charcoal layers. In each case there was a gentle slope from the source of the coarse materials to the pavement.

Near the southern edge of the Thomson Bay dunes is a prominent morainal feature consisting of unsorted boulders, gravel, and sand (Figure 26). The substrate between the boulders consists of a mixture of gravel and sand to a depth of 35 cm. Downslope from this deposit, however, the surface is covered by a single layer of gravel overlying a sand matrix more than 50 cm deep containing only occasional coarse inclusions. This ridge is thought to be a drumlin which was incompletely reworked by wave action on the receding shore of Lake McConnell and then was deflated by wind and gravity during the past 500–700 years (see radiocarbon dates).

Gravel pavements prevent the wind from molding the sand but they do not prevent the removal of the fine fraction from the surface. The deflation that takes place leads to a flattening of the surface much as occurs in the dispersal of sand mounds by strewing gravel on them (Lettau & Lettau, 1969).

All of the major dune areas south of Lake Athabasca contain gravel pavements. In the William River dunes the oblique ridge dune field is located on a more or less flat gravel pavement (Figure 25). The southern and western portions of the Thomson Bay dunes support gravel pavements on a variety of topographic features from ridges to small hills and gently undulating surfaces. Ridges parallel to the present shoreline covered with gravel pavements are exposed in the Wolverine Point dunes. In the MacFarlane River dunes, gravel pavements are common in the southern part of the area at elevations up to 305 m. In all areas pavements are often exposed in the slacks between dunes.

Figure 28. Wet dune slack in the Maybelle River sand dunes. Numerous seedlings of jack pine and birch grow in this slack. A young tree of *Betula papyrifera* is growing on the slope in the foreground along with mats of *Hudsonia tomentosa* and small jack pine saplings.

The pavement stones are often abraded and polished to form ventifacts (Figure 27). Some ventifacts are of the single-ridged type, having been worked on a single surface, others have two winderoded surfaces, and many are of the three-ridged dreikanter type. Mabbutt (1977) stated that ventifacts are less common than the literature may suggest and, except in certain exceptional areas, they characterize pavements of considerable age. Ventifacts have been produced and are still being produced in glacial outwash areas (Antevs, 1928 cited in Cooke & Warren, 1973) and from Pleistocene gravel-mantled surfaces in Wyoming (Sharp, 1949 cited in Cooke & Warren, 1973). South of the presently active sand dune areas, ventifacts were seen by our parties in the Wolverine Point area and south of the headwaters of Ennuyeuse Creek. Tremblay (1961) also reported ventifacts from a large area in northern Alberta and Saskatchewan (see above). The age of the ventifacts in the Lake Athabasca sand dunes is unknown but they were certainly cut and polished after or during the time the postglacial lakes were draining. Provided our surface age calculations are approximately correct they would have been formed in about the last 4200 years.

Dune Slacks

The flat interdunal areas or troughs between sand ridges are called dune slacks. This name was used by Tansley (1953), p. 861), who defined them as "damp or wet hollows left between dune ridges, where ground water reaches or approaches the surface of the sand." Laing (1958, p. 214) used the term *panne* for similar feature that he described as "moist, flat surfaces, and blowout pond margins." The moisture condition of dune slacks in the Lake Athabasca sand dunes varies from standing water to dry sandy flats and gravel pavements. In some places the lowest level to which deflation takes place between dune ridges is determined by the water table and these places may hold small ponds or moist flats (Figure 28). If the base level of the slack is determined by a gravel pavement or by a

Figure 29. Dry dune slack in the Thomson Bay dune field. The brownish, silty-clay soil is broken into irregular polygons and the cracks are filled with sand to about 25 cm. Few plants grow in this habitat except for scattered individuals of *Deschampsia, Elymus,* and *Tanacetum.*

silty-sand hardpan layer the slack may be dry (Figure 29). The moisture level of slacks varies with the season and some that hold standing water in spring are dry during midsummer and may be moist again in the fall. Sand accretion may also influence the moisture condition of a dune slack. Sand may accumulate in a slack by general infiltration over the entire surface, thereby slowly raising its general level, or a dune front may invade the slack from its edge and rapidly modify the moisture characteristics of a part of the slack. Ranwell (1959) described the moisture regime of dune slacks and recognized a gradient from wet to dry. He noted that the extremes differ greatly in their floristic composition. Wet to moist dune slacks provide a good habitat for seed germination and seedling establishment (see below), and the flora of these slacks, consequently, is the richest of any of the dune habitats; dry slacks, on the other hand, have few species and are sparsely plant covered.

Wet to moist slacks are usually confined to the periphery of dune fields or to partially buried drainageways within them. Some dune fields, for example at Wolverine Point, do not seem to have wet or moist slacks except perhaps in the very early spring.

Stabilized Aeolian Topography

Aeolian topography has already been mentioned in describing the lands adjacent to the open sand areas. This topography is widespread south of Lake Athabasca. Throughout this region there is a complex system of ridges, dunes, sandy plains, and muskeg, with occasional lakes, ponds, and shallow stream valleys. The studies by Sproule (1939), Tremblay (1961), and David (1981), discussed above, treat certain phases of it, but ground exploration is much needed. If the general frame of reference used in the present paper is tenable, the whole system should have been developed

mainly by shore processes and wind as the shore of Lake Tyrrell–McConnell retreated northward across the drift-covered plain of the Athabasca Sandstone.

The only kinds of vegetation that now appear capable of stabilizing the sands are dry upland forests and wet lowland forests and meadows and, even in an otherwise forested landscape, such vegetation does not become established in the presence of high winds. We do not know when pine forests reached the shores of ancestral Lake Athabasca, but probably it was not until after the close of the xerothermic interval with its warm dry climate. It is possible, however, that gallery forests advanced down river valleys during this interval (see above).

Some of the present more or less stabilized topography is clearly visible in the oblique aerial photograph shown in Figure 14. The view is northeasterly from a point 6.5–8 km southeast of Wolverine Point, with the mouth of MacFarlane River at the upper right corner of the picture. The photograph shows a series of more or less parallel ridges running east and west and stopping at the shallow valley of the small stream that enters the lake at the next point east of Wolverine Point. The ridges fork in several places and show many gaps in their continuity. Other photographs, taken from points farther east, show the small stream with an eastern branch, flowing through a broad sand plain, with some ridges continuing eastward on its far side. The sand plain ends near the lake shore with a series of more recent shore ridges. The east–west ridges are composed mainly of sand, but some have gravel in them. They are extensively blown out, so that in many places they have become merely ranges of sand hills. The blowouts tend to be orientated diagonally to the trend of the ridges, like those described above nearer the shore of the lake. Ventifacts were found near the top of one of these hills, apparently in place and with lichens growing on them.

Between the east-west ridges in Figure 14 is a system of lobate ridges generally trending north and south. Though variously curved, most are convex eastward. On the ground these ridges proved to have a well defined dune pattern with steep slopes facing east and long gentle slopes and tongues to the west. The position of the slip faces indicates that they were formed by westerly winds. Thus they have the form of parabolic dunes. They are so much altered by blowouts that in places they can hardly be called ridges. Rather they are ranges of hills, some of which retain a ridge form.

The long east–west ridges appear, in many cases (Figure 57), to be border ridges that mark the track of a parabolic dune. In some cases they may be moranic in origin (see above) as is a ridge south of the Thomson Bay dune field (Figure 6). We do not know whether the terrain southeast of Wolverine Point was formerly in a large dune area. If so, the parabolic dunes did not form until after it became at least partly stabilized.

The topography of the region south of the William River dune system suggests that it was once an open dune area that has since become stabilized and covered by forest. Further evidence was obtained along the winter road to Cluff Lake, about 3 km south of the present open dune field; where a gravel-covered surface containing ventifacts was exposed by road-building equipment. These ventifacts resemble those presently forming on the open gravel pavements.

The Vegetation of the Sand Dune Region

Plant habitats within the areas of actively blowing sand can be defined only on an *ad hoc* basis. Physical disturbance is virtually continuous, though its intensity varies widely in space and time. Migrating dunes override all other plant habitats that stand in their way. Small water bodies are filled with sand and their marginal zones of vegetation buried. Small drainage systems are pushed into new channels or eliminated. Mature forests whether dry or wetland types, are killed and buried. Even those habitats that have an appearance of permanence, such as isolated stands of mature trees or dune slacks that contain well developed muskegs, may be highly modified or completely eliminated by the moving sand. The changes commonly occur within the life-spans of most of the plants that make up the vegetation found at a given point in time.

Habitats in the more or less stabilized areas among the dune fields and immediately south of them are here defined by the vegetation found in them: forest (dry, intermediate, and wetland), muskeg shrub, muskeg meadow, grass-sedge meadow on sand, and aquatic vegetation.

In describing the vegetation we have avoided the use of terms such as "community" and "association" that imply a greater knowledge than we have about interrelationships among plants grow-

ing together. For these terms we have substituted the word "assemblage." For the term "dominant" we prefer to use "primary" for the species that characterize assemblages and make them physiognomically discernible from their neighbors.

We have also avoided interpretations of biological succession in our discussions of vegetation. Our main reason is that we have no evidence of succession based on direct observation over time and it would serve no purpose to speculate from the spatial arrangement of plant assemblages. The problem posed by assumptions of succession in sand dune regions have been described by Olson (1958, p. 167) who wrote "Successions in the dunes are going off in different directions and have different destinations according to the many possible combinations of independent variables which determine the original site and subsequent conditions for development...." Ranwell (1972, p. 194) in commenting on the succession diagrams that are commonly included in books on sand dune ecology, concluded that they "...not only oversimplify the many directions in which a particular community can develop, but tend to falsify the reality of the situation in the minds of student ecologists."

Actively Blowing Sand

The vegetation of areas of actively blowing sand is made up of relatively few species, but they occur together in many combinations. The groupings that do occur are the result of many factors, including the chance establishment of species in habitats suitable for their germination and growth, the length of time that the habitat was available for colonization, the rate of sand movement, and the way in which the individual species responds to sand infiltration, to burial, and to erosion. The cycle of sand accretion and the burial of plants followed by sand ablation and excavation of plants is repeated throughout the area of actively blowing sand.

It has been observed that the dune flora decreases in richness (number of species) from the borders of the large dune fields toward their centers. The largest numbers of taxa are in the dune slacks, particularly those with bottoms at or near the water table. Most of the moist to wet slacks are near the southern and northern margins of the large dune systems. Therefore, the decline in species numbers toward the center of the fields is related in part to the absence of suitable slacks which provide a seed bed for many species and to the intensity of sand activity there.

Heights above the general level reached by vegetation on the active dunes are less than 15 m (Hermesh, 1972). On most of the dune surfaces above heights of 3–3.5 m the plants are widely scattered or absent.

Related to the open dune habitat, and apparently with an even more rigorous environment, are the sand surfaces covered with gravel pavement. The vegetation of gravel pavement is very sparse and there are large areas that have no plants at all. Hills covered with gravel pavement may remain uncovered by sand for relatively long periods of time and here a sparse flora, consisting mainly of taprooted perennials, may occur for a while within a field of active sand dunes.

About 30 species and infraspecific taxa of vascular plants were found growing on active dunes that were upwards of about 1 m high. Ten of these are endemic to the area. There appears to be a relationship between the sizes of the six dune areas we have studied and the distribution of the 30 taxa. The largest of the areas (William River) contains 27. The Thompson Bay field has 24 and the MacFarlane River area has 20. The Wolverine Point dunes have 19, the Archibald Lake area 13, and the Maybelle River dunes 9. Parabolic dunes, represented in the above by the last three areas, are notably poorer in endemic plant taxa than are the larger dune fields.

The flora of the Maybelle River sand dunes differs in other respects as well. Here the arctic taxa of the gravel pavements, *Silene acaulis*, *Arabis arenicola*, *Carex maritima*, and *Armeria maritima* ssp. *interior*, and the prominent slack plant, *Juncus arcticus* ssp. *littoralis*, which occurs in the Saskatchewan dunes are absent. *Stellaria arenicola*, otherwise known from sand dunes in Saskatchewan, is present. Chinnappa and Morton (1976) have shown that the characters that distinguish this species appear at random throughout the range of *S. longipes*. While the occurence of *S. arenicola* in the Maybelle River dunes might be interpreted as evidence of a former connection between the Saskatchewan and Alberta dunes it more likely represents a more widespread occurrence of this genotype than had previously been thought.

On the other hand there are species in the Maybelle River sand dunes that are not known to occur in the Saskatchewan dunes. In the Alberta dunes *Agropyron smithii*, *Koeleria macrantha*,

Salix lutea, and *Tanacetum huronense* var. *bifarium* occupy the same habitat as species in the Saskatchewan dunes with comparable ecological requirements. The latter two taxa are closely related to the Saskatchewan endemics *Salix turnorii* and *Tanacetum huronense* var. *floccosum*, respectively, and may represent the taxa from which the endemics have been derived.

Some evidence for the origin and longevity of dune fields is suggested by the distribution of the endemics:

William River sand dunes	10 endemics
Thomson Bay sand dunes	10 endemics
MacFarlane River sand dunes	9 endemics
Wolverine Point sand dunes	4 endemics
Archibald Lake sand dunes	4 endemics
Maybelle River sand dunes	1 endemic

The last three of these areas appear to be formed by parabolic dunes that probably originated as blowouts following fires in pine forests. If our time calculations are tenable, the pine forests did not come into the area until 4000–5000 years ago, while the large dune fields, fed by sand from the William and MacFarlane Rivers, are much older. The Wolverine Point dunes, may have had sufficient time to acquire their few endemics (4), while the more distant Maybelle River dunes, upwind from the large dune fields, got only one. The Archibald Lake dunes are probably younger than those at Wolverine Point but they are nearer the large fields, and downwind from them, and have also acquired four of the endemics.

Seed Germination and Seedling Establishment

Since the original vegetation of the active sand dune areas, if there was any, has been destroyed by sand activity, the present vegetation of these areas must be subsequent to the origin of the dunes. An understanding of the role of vegetation in the formation and stabilization of sand dunes must be based, in part, on a consideration of where and how seedlings become established in an area of active sand.

During the growing season the conditions necessary for seed[3] germination and seedling establishment are soil stability, adequate moisture, and nutrients (Laing, 1958; Ranwell, 1972).

1. Stability. Seedlings of sand dune plants require a certain degree of stability for successful establishment, but they seem to do best in places where sand is slowly accumulating. Seedlings of some plants grow well on or at the base of lee slopes where there is a slow infiltration of sand or in dune slacks that are receiving a general light blanketing of sand. Wagner (1964, p. 94) emphasized that it is places, "with moderate amounts of mobile sand that supports the greatest number of seedlings [of *Uniola paniculata* L.] and apparently provides optimal conditions for their survival and growth." Seedlings are, however, intolerant of microerosion which reduces the available moisture, particularly to adventitious roots, and exposes them to physical damage (Laing, 1958; Huskies, 1977).

2. Adequate moisture. Moist to wet dune slacks and seepage areas at the base of some lee slopes provide sites moist enough for seed germination. Those seeds that germinate on or at the base of lee slopes are usually buried up to 6 cm below the surface. The length of the coleoptile and mesocotyl (the first internode below the coleoptile) of some grasses is proportional to the depth of burial (Laing, 1958). The mesocotyl elongates raising the point at the base of the first leaf where adventitious roots arise, to a position near the soil surface.

Measurements made of mesocotyl length in some dune grasses at Lake Athabasca show that *Agropyron smithii* usually germinates about 3.5 cm below the surface, *Bromus pumpellianus* may germinate at or near the surface or 2 cm below it, *Calamagrostis stricta* agg. germinates at about 2 cm, and *Deschampsia mackenzieana* at about 0.5 cm.

3. Nutrients. The significance of nutrients to seedling establishment was not clear to Laing (1958), who thought that if they were important it might be because of their contribution to an increased rate of growth of seedling roots and consequently a more rapid absorption of water. Seedlings at the base of lee slopes often occur in the organic litter, but this may be due more to the concentration of propagules here by the wind or to the increased water-holding capacity of the soil than to increased nutrients.

Observations were made on the germination and establishment of seedlings in the dune fields around the William River. In general, it was noted that moist to wet dune slacks provide suitable habitats for the germination of the disseminules of

[3]The dry and indehiscent fruits of the Poaceae (caryopses) and the Asteraceae (achenes) are also generally referred to here as seeds.

many dune taxa, including both herbaceous and woody plants. The lee slopes of dunes, particularly those receiving moderate amounts of sand, are suitable for the germination of the seeds of grasses and of a few herbaceous dicots, but seedlings of woody plants have not been seen in this habitat.

1. Moist to wet dune slacks. Our observations show that open moist to wet slacks usually contain numerous seedlings of plants characteristic both of active sand habitats and the surrounding forests and muskegs (Figure 28). Seedlings of active sand dune plants that occur in dune slacks are: *Agrostis scabra*, *Bromus pumpellianus*, *Deschampsia mackenzieana, Salix brachycarpa* var. *psammophila*, *S. planifolia* ssp. *tyrrellii*, *Betula* spp., *Stellaria arenicola, Artemisia borealis,* and *Tanacetum huronense* var. *floccosum*.

Seedlings or gametophores of plants characteristic of stabilized forests and muskegs also occur in moist to wet slacks. These include : *Polytrichum commune*, *P. juniperinum*, *Pogonatum urnigerum*, *Lycopodium inundatum*, *Picea glauca*, *Pinus banksiana*, *Carex aquatilis*, *Juncus brevicaudatus*, *Salix bebbiana*, *S. planifolia* ssp. *planifolia*, *S. pyrifolia*, *Populus balsamifera*, *Betula glandulosa*, *B. neoalaskana*, *Orthilia secunda*, *Andromeda polifolia*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Empetrum nigrum*, and *Hieracium umbellatum*. Some old slacks contain mature forest or muskeg vegetation and the entire flora must be subsequent to the development of such slacks, but all species were not seen as seedlings.

2. Dry dune slacks. Few seedlings occur in dry dune slacks and only seedlings of *Elymus mollis* are common. Seedlings of *Deschampsia mackenzieana* and *Tanacetum huronense* var. *floccosum* were observed growing with *Elymus* on a silty-sand hard pan in a dry slack (Figure 29). Other grasses, including *Agropyron smithii* and *Calamagrostis stricta* agg., have been observed only as adults in dry slacks on hard pan, but their seeds are evidently able to germinate and establish in this habitat. Grasses are the most common plants in this habitat, but some herbaceous dicots notably *Tanacetum* are sometimes locally abundant and *Armeria maritima* ssp. *interior* was seen once in this habitat.

3. Leeward slopes of sand dunes. Some plants have been observed as seedlings on the lee slopes of sand dunes, but whether they can survive throughout the year is in this habitat unknown. The taxa that are known as seedlings in this habitat are: *Agropyron smithii*, *Bromus pumpellianus*, *Calamagrostis stricta* agg., *Hudsonia tomentosa*, *Artemisia borealis*, and *Tanacetum huronense* var. *floccosum*. More commonly, plants establish themselves in the organic litter at the base of lee slopes (Figure 30). Seedlings of the following taxa have been observed here: *Agropyron smithii*, *Bromus pumpellianus*, *Deschampsia mackenzieana*, *Elymus mollis*, *Artemisia borealis*, and *Tanacetum huronense* var. *floccosum*. It is possible that adult plants of these species growing on the lee slopes and crests of active dunes have germinated on the dunes themselves or at the foot of lee slopes. Excavations made at the edge of a dune showed that caryopses of *Agropyron smithii* germinated in a silty-sand hard pan layer in a dune slack and the plants had grown through 10 cm of sand. Further up the slope *Calamagrostis stricta* agg., that had germinated in the same hard pan layer, was growing through 1 m of sand. Woody plants, including *Salix* and *Betula*, do not seem to be capable of germination on active dunes and plants of those genera growing on the dunes (see below) must have germinated in a moist dune slack that was subsequently covered by a migrating dune.

4. Gravel pavements. Seedlings of the following taxa were observed on a gravel pavement: *Salix planifolia* ssp. *tyrrellii, S. silicicola, Silene acaulis, Armeria maritima* ssp. *interior*, and *Artemisia borealis*. In the Thomson Bay dune field individuals of *Arabis arenicola*, *Salix silicicola*, and *Silene acaulis* were seen to be perched 0.8, 5, and 12 cm respectively, above the present gravel surface. The perched plants indicate that either the gravel pavement surface had been eroded between 0.8 and 12 cm during the life of the plants or, more likely, that the plants germinated on a superficial sand layer that was subsequently removed.

The gravel pavements seem to be unfavorable for seed germination and seedling establishment. Their dry condition throughout most of the growing season and their exposure to winds may explain their sparse flora; but *Silene acaulis* and *Armeria maritima* ssp. *interior* are mostly restricted to this habitat. It is probable that their tap-root habit does not adapt them to grow on moving sand; but, in the laboratory, seeds of *Ameria* germinate readily and why seedlings of this taxon do not appear, at least, on moist dune slacks is difficult to explain.

5. Open sand. Seeds rarely germinate on windswept, open sand surfaces and only *Elymus*

Figure 30. Base of the lee slope of a transverse dune in the Maybelle River sand dunes. Organic debris is trapped by *Agropyron smithii* in the foreground. *Calamagrostis, Bromus,* and *Tanacetum huronense* var. *bifarium* occupy the slope.

mollis was observed to do so. Its caryopses germinated as they were being covered with sand moved by a northwesterly wind and the young seedlings were being uncovered by a subsequent northeasterly wind. It is unlikely that these plants could survive continued sand erosion and their survival depended on a change in wind direction.

We have observed that dune slacks provide the main habitat for the invasion of plants into the active dune areas. The seeds of certain herbaceous plants, mainly grasses, are able to germinate and to grow on active dunes, but most of these plants also can become established in dune slacks and may grow up through migrating dune sand. Seedlings of woody plants are known only from moist to wet slacks.

These observations agree with those of Cowles (1899), Ranwell (1972), Laing (1958), *et al.*, in that they emphasize the importance of the dune slack habitat in the vegetation cycles on active sand. Plants undoubtedly have a significant influence on the formation of dunes and can modify their size and shape according to the growth behavior of the colonizing taxa. However, it must be observed that, although plants can function as "dune-formers," dunes can also be formed by non-living features of the landscape such as stones or outcrops or simply by the action of wind on sand. To refer to the sand dunes in the Lake Athabasca region as phytogenic is to overlook this fact. Just as important, however, is the recognition that even when plants do serve to accumulate sand and to modify the form of a dune, they are unsuccessful in this area in permanently stabilizing the sand. The force of the winds along the south shore of Lake Athabasca is great enough that even at a distance of 15 km or more from the lake shore wind is capable of moving sand more rapidly that the vegetation can arrest it.

The Vegetation in Areas of Active Sand

Although the conspicuous and interesting oblique ridge and transverse dunes of the large dune fields command our attention, the most common dune features are the vast areas of sand sheets,

Figure 31. Cushion dunes are formed by clumps of *Deschampsia* and *Bromus* on this gravel pavement in the William River dune field.

rolling sand topography, and small hillock dunes. It is most appropriate, therefore, to begin our consideration of the vegetation of the active sand areas with a look at these features.

Hillock and Cushion Dunes.

Plants and other obstacles are able for a time to trap sand in the form of small dunes. The most common plants to accumulate sand in this way are the grasses *Bromus pumpellianus, Festuca rubra* ssp. *richardsonii, Deschampsia mackenzieana, Calamagrostis stricta* agg., and *Elymus mollis* (Figure 31). Scattered among the grasses may be individuals or small groups of other species characteristic of the open, shifting dunes: *Stellaria arenicola, S. longipes, Artemisia borealis, Achillea lanulosa* ssp. *megacephala,* and *Tanacetum huronense* var. *floccosum.* Most of these dunes are asymmetric in ground plan, with "tongues" directed down wind.

Lens-shaped "cushion" dunes, though they are occasionally barren, are usually formed by the trapping of sand in herbaceous mat plants or by prostrate shrubs. They are most common in areas marginal to the large dune fields or in blow-outs in the adjacent forests. The species most effective in their formation are: *Silene acaulis, Potentilla tridentata, Empetrum nigrum, Hudsonia tomentosa, Arctostaphylos uva-ursi, Vaccinium vitis-idaea,* and *V. uliginosum* (Figure 22). In several localities xerophytic mosses and fruticose lichens replace the vascular plants: *Polytricum commune, P. piliferum, Pogonatum urnigerum,* and species of *Stereocaulon, Cladina,* and *Cladonia.* The cushion dunes commonly harbor a few species from the larger dunes, notably grasses and an occasional willow *(e.g. Salix silicicola)* or if they are near a seed source, seedlings of pine and birch.

Rolling Dune Topography.

In the William River and Thomson Bay fields there are large areas of rolling dune topography. Toward the center of the dune fields herbaceous plants may sparsely cover these dunes while

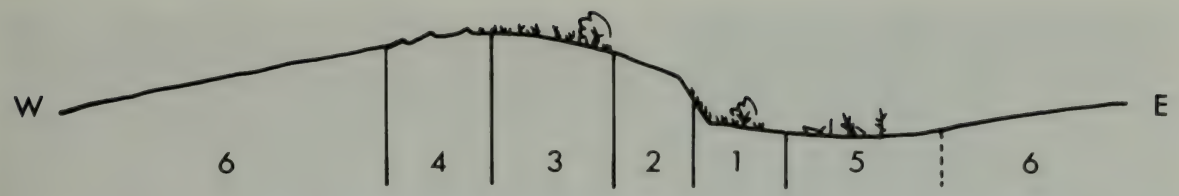


Figure 32. Transect of a transverse dune. The movement of the dune is from west to east.

toward the perimeter of the fields *Salix* and *Betula* are common (Figure 23). The vegetation of these dunes includes all of the plants of active sand dunes, such as: *Bromus pumpellianus* (often a primary species), *Elymus mollis, Deschampsia mackenzieana, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Salix brachycarpa* var. *psammophila, S. silicicola, S. turnorii, S. planifolia* ssp. *tyrrellii, Betula glandulosa, B. neoalaskana, B.* × *sargentii, B.* × *utahensis, Hudsonia tomentosa, Stellaria arenicola, S. longipes, Achillea lanulosa* ssp. *megacephala, Artemisia borealis,* and *Tanacetum huronense* var. *floccosum.*

The differences between herbaceous and shrubby dunes are to be sought not in the dunes themselves but in the establishment requirements of the plants. Many of the herbaceous taxa have been observed to be capable of establishment on the surface of active dunes where moisture may be available only for a short time after a rain or in the form of dew. The woody plants, *Salix* and *Betula,* require a more continuously moist seed bed and relatively stable sand conditions such as prevail in a dune slack that lies at or near the water table. These different plant requirements appear to explain the gradients of poor to rich flora or from no plants to an herbaceous vegetation, then to a mixed woody and herbaceous vegetation, such as has been observed in the major active dune fields. These gradients are understandable in terms of the relatively greater exposure of the water table surface on the perimeter of the dune fields and the harsher environmental conditions that prevail in their centers, primarily in the form of windblown sand which abrades the plants and keeps the habitat unstable.

Transverse Dunes.

Within the active dune fields a cyclical pattern of vegetation establishment, burial, and reexposure is commonly observed. This process is not successional in the sense of leading to a final stage or of each "successive" vegetation that has a profound effect on the habitat, but rather it is cyclical. Most of the species involved become established in the dune slacks and what apparent change is observable in the floristic composition from one "stage" to another is due to the length of time that the depression remains uncovered by a migrating sand dune and to the selective elimination of species as a dune invades the dune slack. A composite transect across a dune slack being invaded by a transverse sand dune will illustrate this process (Figures 32, 33 & 20).

Zone 1. The assemblage of plants in the dune slack and at the foot of the slip face of a dune migrating into a dry depression in the Wolverine Point dunes consists of the following taxa: *Bromus pumpellianus, Festuca rubra* ssp. *richardsonii, Deschampsia mackenzieana, Elymus mollis, Calamagrostis stricta* agg., Salix silicicola, *Stellaria arenicola, Empetrum nigrum, Tanacetum huronense* var. *floccosum,* and *Artemisia borealis.* If one were to name the primary species in this group, or at least the most characteristic, they would be in the genera *Calamagrostis, Deschampsia, Bromus,* and *Elymus.* Most of the plants in the assemblage are on the lower slopes of the slip face or just at its base on the more nearly level ground. Those on the slip face are being covered slowly by sliding sand. Some of those at the base are on small hillocks of sand while others have spread more widely. Most of the taxa are rhizomatous or have decumbent spreading stems, while *Deschampsia* is caespitose.

In a dune slack with an exposed water table, but one which is not flooded throughout the year, zone 1 may take on a different aspect. Moist to wet slacks provide an excellent seed bed for many species (see above) and, if sufficient time elapses before the slack is invaded by a migrating dune, a young forest may develop (Figure 33). Sometimes, however, a dune moves across the slack so soon after the water table is exposed, and the sand moves so rapidly, that no plants occur on the lee slope of the invading dune (Figure 34).

In the MacFarlane River dune field a young forest in a moist slack was observed being invaded by dunes (Figure 33). In this case the older part of the depression (zone 1) was covered by a shallow layer of sand and the seedlings of a number of additional species had become established. Here a young forest developed consisting of saplings of *Pinus banksiana, Betula papyrifera,* and an occasional individual of *Larix laricina.* The ground was covered by a sparse moss mat of *Polytrichum* with *Sphagnum compactum, Aulacomnium palustre,* and *Drepanocladus uncinatus* along with the vascular plants *Calamogrostis stricta* agg., *Carex abdita, Juncus arcticus* ssp. *littoralis, Hudsonia tomentosa, Potentilla tridentata, Empetrum nigrum, Artostaphylos uva-ursi* var. *coactilis, Vaccinium uliginosum, Hieracium umbellatum,* and *Solidago decumbens* var. *oreophila.*

Zone 2. The sand moving up the long gentle slope from zone 6 is carried over the top of the dune and deposited in zone 2. This zone, on a dune invading a dry slack, may be devoid of plant life. The herbaceous plants that may have been rooted in the dune slack are usually not able to withstand the rapid accumulation of sand in this zone and soon succumb. If the dune, however, is invading a moist-wet slack in which woody plants have become established, shrubs may occupy this zone because of their ability to withstand the rapid sand accummulation (Figures 33 & 20).

Figure 33. Panorama of a large dune slack in the MacFarlane River dune field. The slack is being invaded by two dunes. The foreground dune is moving from the west northwest (away from the viewer), the dune in the middle distance is moving from the south southeast (from right to left), and the windward slope in the upper left is moving from the west (to the left). In the slack, which has remained undisturbed for some time, a young jack pine-birch woods is being buried by sand. Birch trees survive on the lee slope and the crest of the dune on the left, and *Salix planifolia* ssp. *tyrrellii* appears on the crest of the dune in the foreground. Seedlings become established in the slack around the perimeter of the forest, especially in a moist area near the base of the windward slope.

Figure 34. Transverse dune about 15 m high invading a moist dune slack near Yakow Lake. The rate of advance of the dune appears to be so rapid that the plants growing in the slack fail to grow up through the lee slope.

Zone 3. The lee side of the top of the dune (Figures 33 & 20) may be sparsely plant-covered. *Bromus pumpellianus* and *Deschampsia mackenzieana* are usually the most abundant plants in this zone; *Elymus mollis* and *Festuca rubra* ssp. *richardsonii* are common; and *Stellaria arenicola, Tanacetum huronense* var. *floccosum, Artemisia borealis, Salix planifolia* ssp. *tyrrellii,* and *Betula papyrifera* are occasional.

In some places (Figure 33) a well developed thicket may occupy the lee slope and crest (zone 3) of an active dune. This vegetation may include a number of willows (*Salix silicicola* and *S. turnorii*) and birches (*Betula glandulosa, B. neoalaskana, B. occidentalis, B.* × *sargentii, B.* × *utahensis,* and *B. winteri*) in addition to the previously mentioned species.

The vegetation on transverse dunes in the Maybelle River dunes of Alberta is physiognomically similar to that on the Saskatchewan dunes but the species are different. The most common species on the crests and lee slopes (zone 3) of the dunes in this region are: *Agropyron smithii, Bromus pumpellianus, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii,* and *Tanacetum huronense* var. *bifarium;* of less importance are: *Koeleria macrantha, Hudsonia tomentosa,* and *Artemisia borealis.* In some places shrubs or small trees may appear, including, most commonly, *Salix lutea, S. planifolia* ssp. *planifolia* and *Betula papyrifera, B.* × *sargentii,* and *B.* × *winteri.*

Zone 4. The deflation zone on the windward side of the dune crest is occupied by scarcely any living plants. It is notable for small hummocks of sand (Figure 35) held together by the remains of a group of grasses that appeared in zone 3. The hummocks are capped by tangles of dead leaves and stems. Digging in them revealed dead roots and stem bases of the grasses, with only a few dead roots that had penetrated below the general level of the dune surface. This suggests that although the plants in zone 3 appeared to be thriving, the eastward advance of the dune crest will place them on its windward side where they are subject to erosion and ultimately will be killed. Only the sand immediately around their roots would be held for a time forming hummocks as the general surface is eroded. As the erosion continued on the windward

Figure 35. Irregular hummocks mark the remains of *Elymus* and *Calamagrostis* left behind on the windward side of a transverse dune.

Figure 36. Transverse dune on the right invading (from right to left) a dry, gravel covered dune slack in the MacFarlane River dune field. Skeletonized jack pine, killed during a previous sand invasion, appear on the windward slopes in the foreground.

Figure 37. Birches being undercut and killed as their dune is reduced by ablation in the Thomson Bay dune field.

slope of the dune, the hummocks become smaller and finally disappear completely. There is here the suggestion that the assemblage in zone 3 in temporary and superficial, with no deep penetration of the dune sand. In other places where woody plants occupy this zone the penetration is deeper, presumably to the surface of the original dune slack; but even in these cases the vegetation appears to have only a small effect on the rate of movement or the form of the dune. It may serve only to increase, somewhat, the deposition of sand on the upper part of the lee slope, and to lengthen the slope to the top of the slip face.

Zone 5. Where the surface wind again becomes effective and the dune slack approaches or reaches its lowest level, skeletal remains of old forests are uncovered (Figure 36) and individuals of birch and willow may remain perched on hillocks of sand (Figure 37).

Oblique Ridge Dunes.

The high oblique ridge dunes have plants only on their lee slopes and sometimes on the secondary dunes that radiate from their windward slopes. No plants occur on or near the dune crests and only rarely do any plants extend more than one half way up the lee slopes; plants usually occur less than 3 m above the base of the dune (Figure 38). Only herbaceous plants occur on these dunes including: *Deschampsia mackenzieana, Elymus mollis, Bromus pumpellianus, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Tanacetum huronense* var. *floccosum,* and *Artemisia borealis.* Seedlings of *Deschampsia, Elymus, Bromus,* and *Artemisia* were observed to be growing at the foot of the lee slopes. At the ends of the oblique ridge dunes, where the sand is less deep and the slope is less steep, seedlings of *Bromus* have been observed and presumably other herbaceous species could also become established here.

Figure 38. Lower part of the lee slope of an oblique ridge dune in the William River dune field. *Tanacetum, Calamagrostis,* and *Bromus* grow on the slope. The oblique ridge dune in the background has two prominent peaks.

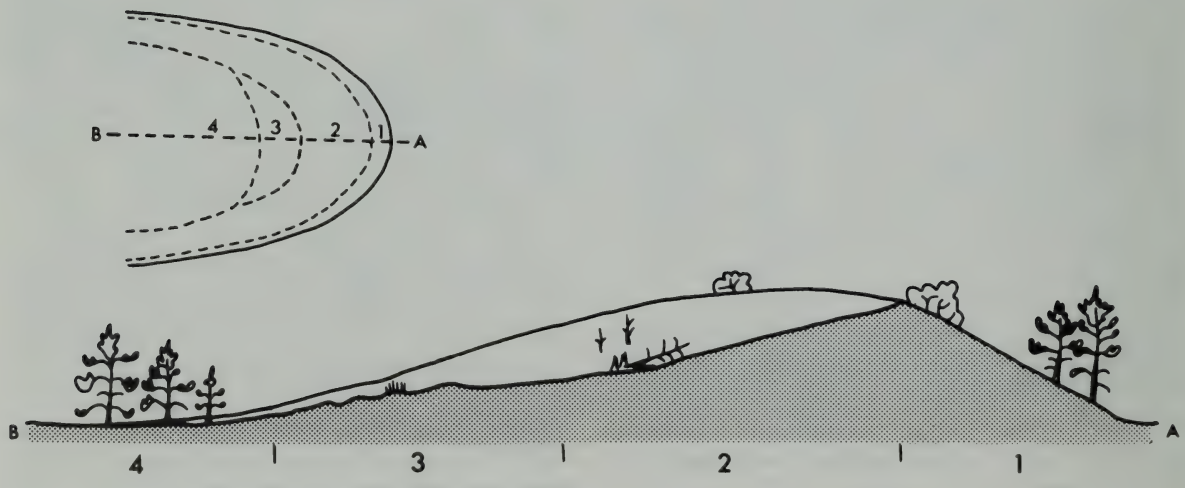


Figure 39. Parabolic dune. Plan view and cross-section subdivided into zones.

Parabolic Dunes.

The parabolic dune cycle is similar in many respects to that described for the transverse dunes and its lee slope is comparable to the precipitation ridge that forms on the perimeter of the major dune areas where sand is actively invading the surrounding vegetation.

The vegetation of the parabolic dunes can best be described by a composite example based on dunes studied in the southerly parts of William River and Thomson Bay fields. The cross-section of a parabolic dune is illustrated in Figure 39. The lee slope may be invading *Pinus banksiana* forest, *Picea mariana* muskeg or open wetland vegetation. The dune crest may stand between 6 and 9 m above the surface of the vegetation that it is invading. If trees impede the movement of wind and sand, the dune crest builds to a higher level than if no obstacle were present. If the obstacle is removed, for example by fire, the dune crest blows out and moves ahead more rapidly, seemingly impeded only by *Betula,* which may grow as a shrub through its crest, and mats of *Hudsonia* which attempt to recolonize its slopes. Both of these impediments are soon overcome, however, and the survivors bypassed.

Along the lee slope (zone 1), certain species have the ability to grow up through sand that accumulates on the dune face before they are overwhelmed. If the sand is invading a pine forest (Figure 15), *Pinus banksiana* trees may survive burial for a while, and *Arctostaphylos uva-ursi, Betula occidentalis, B. papyrifera, B.* × *sargentii, B.* × *utahenses, B.* × *winteri, Geocaulon lividum, Ledum groenlandicum, Vaccinium uliginosum,* and *V. vitis-idaea* may grow on the advancing dune

Figure 40. Lee slope of a parabolic dune invading a *Picea mariana* muskeg northeast of Little Gull Lake. The muskeg shrubs, *Chamaedaphne calyculata* (foreground), *Andromeda polifolia*, and *Vaccinium uliginosum*, grow up through the sand as it advances. They are associated with the dune plants, *Calamagrostis stricta* agg., *Tanacetum huronense* var. *floccosum*, and *Stellaria arenicola,* which have the ability to germinate on dune slopes.

Figure 41. *Hudsonia tomentosa* is a primary species on the windward edge of a large parabolic dune west of Maybelle River.

slope. None of these species, with the exception of *Betula,* is able to withstand moving sand for long and all are soon overtopped and killed.

If a muskeg is being invaded (Figure 40), *Andromeda polifolia, Chamaedaphne calyculata, Ledum groenlandicum, L. palustre* var. *decumbens, Vaccinium myrtilloides,* and *V. uliginosum* may occupy the dune slope, frequently appearing on the slope as high as 3 m above the forest floor. These are often in association with the dune plants *Achillea lanulosa* ssp. *megacephala, Artemisia borealis, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Stellaria arenicola, Tanacetum huronense* var. *floccosum,* and others. These dune species are not a part of the muskeg flora itself but they become established on the moist sand at the base of the lee slope, or, in the case of *Tanacetum,* on the dune slope itself. These dune plants grow up through the sand along with the few muskeg species as the dune advances. The survival of these individuals in the face of sand accumulation will depend upon their ability to produce roots nearer to the surface and on the rate of slope movement. In some cases, where the slope is devoid of vegetation, we assume that the rate of sand movement was too rapid for the plants to adjust.

The center of a parabolic dune (zone 2) is actively eroding. No plants grow there, and it is studded with the remains of trees that were killed. In some places a depression exposing the surface of the water table may be seen to windward of the erosional area. Here a variety of species, particularly those associated with the active dunes, may become established, including: *Bromus pumpellianus, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Hudsonia tomentosa, Juncus arcticus* ssp. *littoralis, Salix brachycarpa, S. brachycarpa* × *pyrifolia, S. pyrifolia, S. silicicola* (rare), *S. planifolia* ssp. *tyrrellii, Betula* spp., and *Tanacetum huronense* var. *floccosum.* With the exception of *Hudsonia* and *Calamagrostis,* these species do not occur in the pine forests that may eventually invade and occupy this kind of site.

The usual pattern of plant invasion along the windward margin of the parabolic dune (zone 3) (Figure 41) involves mats of *Hudsonia tomentosa*

Figure 42. Border ridge extending from the southwestern tip of the parabolic dune west of Maybelle River (cf. Figure 53). The gentle sand slopes are sparsely covered by open grown jack pine, *Hudsonia tomentosa*, *Polytrichum* spp., and fruticose lichens.

(primary), *Arctostaphylos uva-ursi, Artemisia borealis, Festuca rubra* ssp. *richardsonii, Empetrum nigrum,* and *Polytrichum commune,* together with seedlings of *Pinus banksiana* and *Betula* spp. The first trees of *Pinus banksiana* to grow at the edges of the stabilized area (zone 4) are characteristically of a bushy, open-grown form. In the forest that follows, this form is accompanied by slender, less profusely branched trees (Figure 46). The forests and other vegetation that become established on stabilized parabolic dune surfaces will be discussed below.

The border ridges that trace the path of movement of parabolic dunes across the landscape are very sparsely covered by *Pinus banksiana* and an almost continuous moss mat of *Polytrichum* spp. (Figure 42). The only other important species is *Hudsonia tomentosa.* Between the patches of open sand may occur occasional individuals of *Festuca saximontana, Salix bebbiana, Betula papyrifera, Prunus pensylvanica, Arctostaphylos uva-ursi,* and small patches of fruticose lichens.

The simple parabolic dune situation that has been discussed often is made more complex by the formation of blowouts in the forest on the windward side and the possible development of these blowouts into parabolic dunes. The dune crest may be broken through by a blowout or by the removal of impeding trees and a secondary parabolic dune may become superimposed on the main dune. In places where parabolic dunes may cover an extensive area, such as at Wolverine Point and Maybelle River, the open sand area is so large that it contains transverse dunes, rolling dunes, and other features of the major dune fields. The vegetation of these features is similar to that described above.

Gravel Pavements.

The plains and rolling hills of sand that are covered with a veneer of stones are sometimes sparsely covered with plants, but large expanses are devoid of plant life (Figures 24 & 25). Those species that do occur on the gravel pavements are widely scattered and include: *Carex maritima* (rare), *Salix brachycarpa* var. *psammophila, S. silicicola, S. turnorii, S. brachycarpa* × *turnorii, Silene acaulis, Arabis arenicola, A. lyrata, Armeria maritima* ssp. *interior, Artemisia borealis,* and *Tanacetum huronense* var. *floccosum.* Evidently

Figure 43. Hummocks of *Silene acaulis* on a gravel pavement in the Thomson Bay dune field. A plant of *Salix silicicola* is visible at center right.

these flowering plants are able to germinate and become established on the gravel pavements, but seedling are rarely observed (see above).

The mosses *Polytrichum juniperinum* and *P. piliferum* form large mats in some areas. On stones and boulders grow the lichens *Acarospora smaragdula, Buellia lacteoides, Evernia mesomorpha, Hypogymnia physodes, Lecanora badia, L. chrysoleuca, L. polytropa, Lecidea auriculata, Parmelia disjuncta, P. stygia, Rhizocarpon riparium, Rhinodina* sp., and *Umbilicaria hyperborea.* Other lichens such as *Stereocaulon alpinum* and *S. condensatum* may form cushions on thin sand layers on the gravel. Some saxicolous lichens on the gravel pavements appear as unattached vagrant lichens (Weber, 1977), and form pebble-like balls that lie free on the pavement surface. This unusual morphological modification is known in the Lake Athabasca area only from the gravel pavements in the sand dunes surrounding the William River and occurs in *Cetraria hepatizon, Lecanora chrysoleuca, L. melanopthalma, Parmelia stygia,* and *Xanthoparmelia centrifuga.*

Some gravel pavement surfaces appear to be relatively stable and hummock-forming plants such as *Silene acaulis* tend to build up hillock dunes on them (Figure 43). The occurrence of perched plants, however, indicates that deflation of the surface occurs as sand is winnowed from between the stones or as shallow sand layers are eroded. In addition to the perched plants of *Arabis arenicola* and *Silene acaulis,* noted above, a 12- to 14-year old plant of *Salix brachycarpa* was observed perched about 15 cm above the present surface indicating a deflation rate of the gravel surface, or of a shallow sand layer, of about 1 cm per year.

In places where there is a slow infiltration of sand over the gravel-covered surface the mosses *Pogonatum urnigerum, Polytrichum juniperinum, P. piliferum,* and *Rhacomitrium canescens* may form mats (Figure 44), sometimes accompanied by *Silene* hummocks and by *Salix silicicola.*

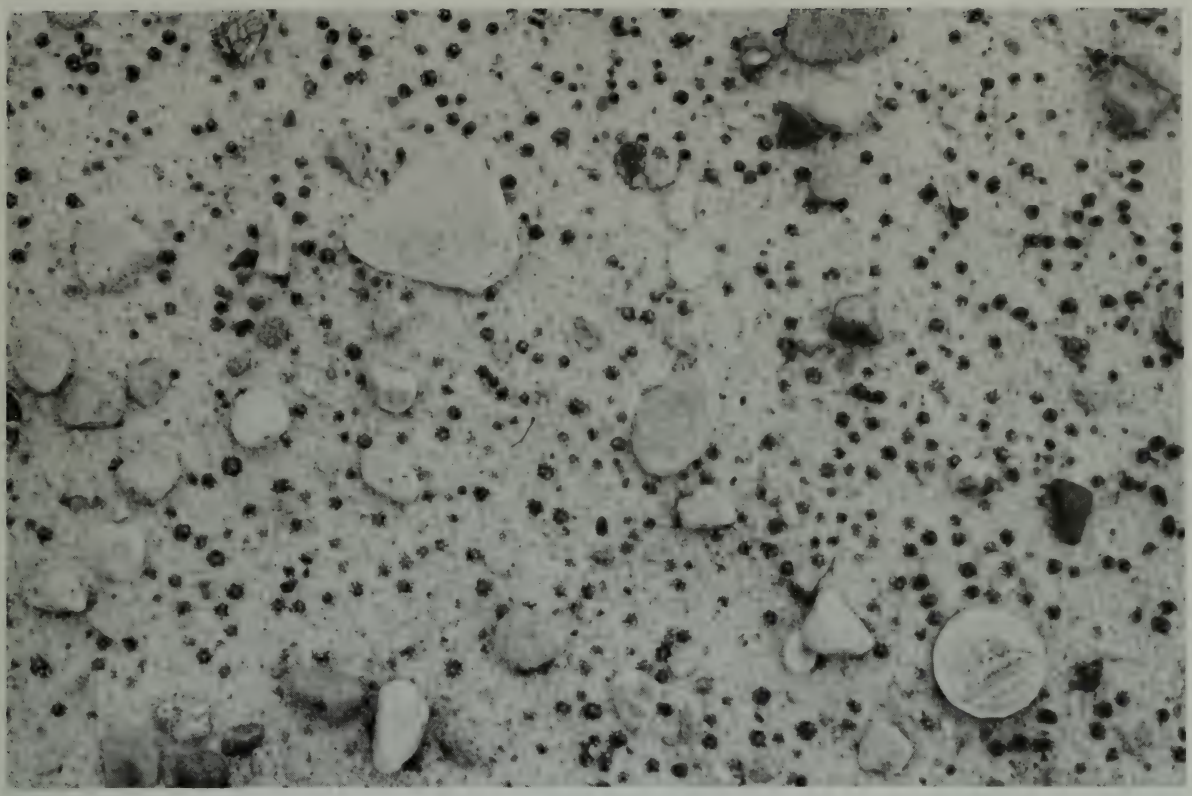


Figure 44. A gravel pavement composed of gravel and a mat of *Polytrichum juniperinum*. The pebbles moved onto the moss mat by downslope creep.

In areas where the sand has built up into shallow dunes the tap-rooted plants of the gravel pavements, *Silene acaulis, Arabis arenicola, A. lyrata,* and *Armeria maritima* ssp. *interior,* do not occur; but, rather, an assemblage of sand dune plants, including *Festuca rubra* ssp. *richardsonii, Stellaria arenicola,* and *Empetrum nigrum,* predominate (Figure 45).

There are extensive areas of sandy-gravel pavement in the southwestern part of the William River dunes and in the southern part of the MacFarlane River dunes where colonization by *Empetrum*, forming mats and hummocks, is accompanied by open stands of *Pinus banksiana* and *Betula* × *sargentii* (Figure 46). *Empetrum nigrum* covers the shallow sand as mats or, as sand accumulates on the mats, as small hummocks. These hummocks are accompanied by other hummock-forming species, *Hudsonia tomentosa* and *Potentilla tridentata.* Interspersed among these hummocks are *Bromus pumpellianus, Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Salix silicicola, Stellaria arenicola, Prunus pensylvanica, Vaccinium uliginosum, Achillea lanulosa* ssp. *lanulosa* and ssp. *megacephala, Artemisia borealis,* and *Tanacetum huronense* var. *floccosum. Pinus banksiana* may slowly invade the area over a period of time and individuals ranging from seedlings about five years old to trees 4 m tall and 18 cm in diameter at the base may be seen. Here *Pinus* grows in bushy habit typical of open-grown plants (Figure 46). Under trees develop mats of *Stereocaulon alpinum, S. glareosum, Cladonia amauracraea, C. uncialis,* and *Cetraria nivalis. Betula occidentalis, B.* × *sargentii,* and *B.* × *winteri* also invade the stabilized *Empetrum*-moss mat as individuals or as small populations.

The generally flat *Empetrum*-moss mat covered surface may be broken by small blowouts and dunes. One such dune, standing 1.8 m above the surface, supported a typical sand dune flora consisting of *Bromus, Festuca, Calamagrostis, Hudsonia, Stellaria, Artemisia,* and *Tanacetum.* The absence of *Empetrum* mats on the dune probably reflects its inability to grow under conditions of rapidly accumulating sand which would lead to dune formation. When a shallow sheet of sand covers an area, populations of *Calamagros-*

Figure 45. Shallow sand dune trapped by hummocks of *Empetrum nigrum* and the grasses *Bromus*, *Calamagrostis*, and *Festuca* overlying a gravel pavement in the MacFarlane River dunes.

tis, Deschampsia, and *Festuca* tend to predominate over those of *Empetrum,* which can survive only for a short time by modifying its growth to a hummock or a mat of branches that protrude to the surface.

Another kind of gravel-covered surface occurs as old raised beaches covered with flat stones derived from the prevailing thin-bedded sandstone bedrock of the region, though occasionally other rocks, probably derived from glacial tills, are represented. These low ridges are nearly devoid of vegetation. Occasional individuals of *Arabis lyrata, Artemisia borealis,* and *Silene acaulis* were found rooted in sand among the stones. *Arabis* and *Artemisia* occur also on sand beaches at the lake shore, but *Silene* has thus far been seen only in the dune areas.

Dune Slacks and Buried Drainageways.

The moisture regime of dune slacks ranges from open water to dry sand or gravel pavements (see above), and the vegetation varies accordingly. Dry slacks support few taxa, including those grasses and herbaceous dicots able to germinate there. In moist to wet slacks a rich flora may develop that includes not only dune plants but also plants of the surrounding forests and muskegs.

In slacks with exposed water tables (Figure 28), but which are not flooded throughout the year, the entire surface may become covered with seedlings. In the early stage of development the vegetation is graminoid and may be dominated by *Agrostis scabra, Deschampsia mackenzieana* and *Juncus arcticus* ssp. *littoralis* associated with *Calamagrostis stricta* agg., *Festuca rubra* ssp. *richardsonii, Carex abdita, Juncus alpinus, Salix brachycarpa* var. *psammophila, S. silicicola, S. turnorii, S. planifolia* ssp. *tyrrellii,* and *Stellaria arenicola.* The mosses *Drepanocladus exannulatus, Pohlia drummondii, P. nutans,* and *Polytrichum commune* may appear also at this stage along with seedlings of *Pinus banksiana, Betula papyrifera,* and *B.* × *sargentii.* A tree cover may develop if sufficient time elapses before the dune slack is invaded by a sand dune.

In the southern part of the William River dune system there is a complex of dunes and depressions that appears to represent partly buried

Figure 46. Open jack pine-birch stand on a gravel pavement in the William River dune field. *Betula neoalaskana*, *B. occidentalis*, and *B.* × *sargentii* are co-primary with *Pinus banksiana*. Mats of *Empetrum nigrum* and *Polytrichum* spp. are scattered between the trees.

drainageways (Figure 47). These drainageways occur as moist to wet, or sometimes dry, depressions located between active dunes. One small area at the southwestern edge of the dune system was studied. Here the sand was moving southward, invading a *Pinus banksiana* forest and a *Picea mariana* muskeg and forming a precipitation ridge. A profile through a portion of the dune and depression complex is illustrated in Figure 48. The precipitation ridge on the right and the dune invading from the left (zones 1 & 8) both supported thickets of *Betula neoalaskana, B. papyrifera,* and *B.* × *sargentii.* Of all the dune species, the birches are best able to withstand burial by deep sand deposits. Even those plants that survive, however, will be killed eventually as the dune moves past them and ablation of the sand occurs (Figure 37).

To windward of the precipitation ridge was a low rolling dune (zone 2). It was primarily covered by *Calamagrostis stricta* agg., which occurred with *Bromus pumpellianus, Festuca rubra* ssp. *richardsonii, Carex aquatilis, Juncus arcticus* ssp. *littoralis,* and *Tanacetum huronense* var. *floccosum.* No seedlings were seen on this dune. On the windward side of the low dune was a dune slack (zone 3) that was in the process of being filled with sand and was not conspicuously wet. This depression was covered by a mat of *Polytrichum commune* and *Pogonatum urnigerum.* Growing in this mat were: *Calamagrostis stricta* agg., *Carex aquatilis, Juncus arcticus* ssp. *littoralis, Salix brachycarpa* var. *psammophila, S. planifolia* ssp. *tyrrellii, Betula glandulosa, B. papyrifera, Potentilla tridentata, Empetrum nigrum,* and *Achillea lanulosa* ssp.

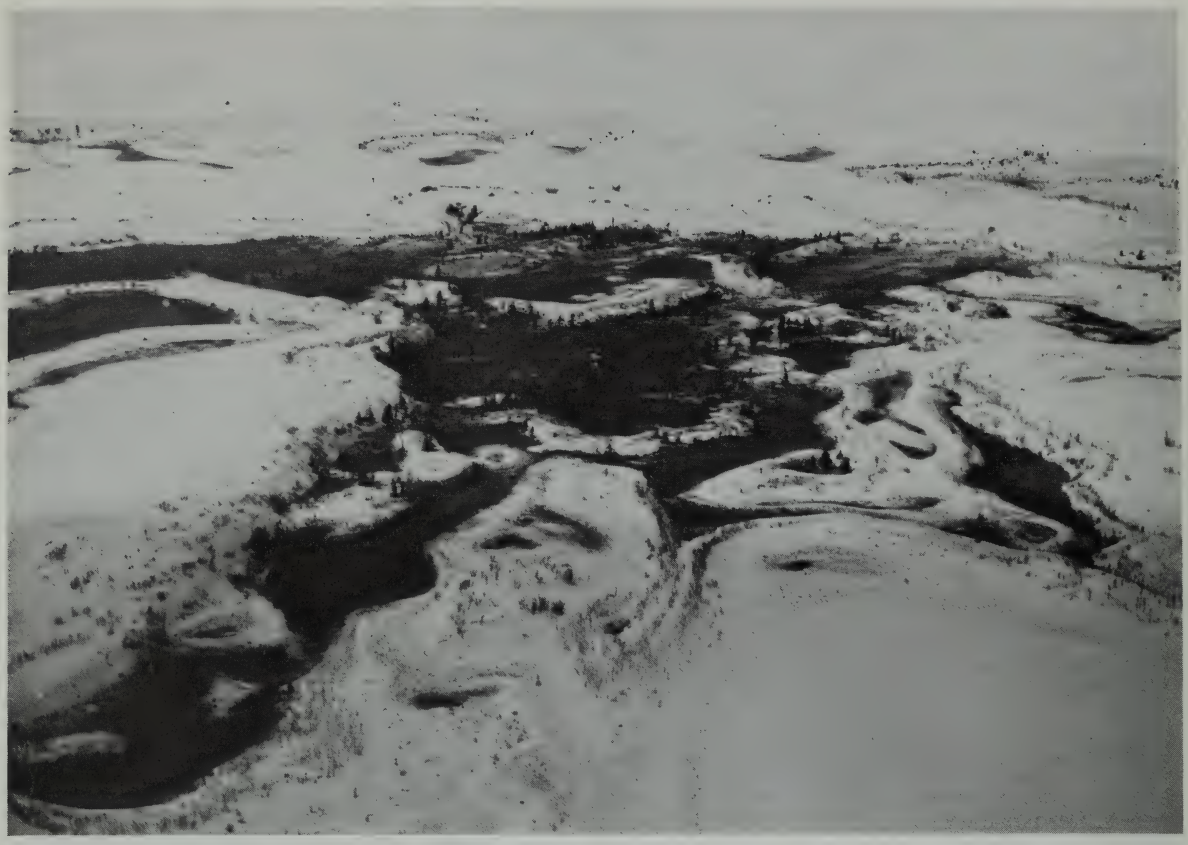


Figure 47. Oblique aerial view of a wet drainageway in the William River dune field.

megacephala, seedlings of *Pinus banksiana, Carex aquatilis, Artemisia, Tanacetum,* and several grasses.

Invading the depression was a shallow sand dune (zone 4) covered with *Calamagrostis stricta* agg., *Carex aquatilis*, *Juncus arcticus* ssp. *littoralis*, *Salix brachycarpa* var. *psammophila*, *S. pyrifolia, S. planifolia* ssp. *tyrrellii, Silene acaulis* f. *athabascensis* (very rare), *Tanacetum huronense* var. *floccosum*, and young plants of *Pinus banksiana*. Shrubs of *Betula glandulosa* were buried by about 2–4 cm of sand. There were no evident seedlings on this dune, the windward slope of which was being eroded by the wind. Some plants were being eroded out and killed.

Still further windward is another dune slack that was seasonally wet (zone 5). The primary vegetation in this slack was a mat of *Pogonatum urnigerum* and *Carex aquatilis* along with *Betula glandulosa* and *Lycopodium clavatum*, *L. inundatum*, *Pinus banksiana, Agrostis scabra*, *Salix bebbiana*, *S. pyrifolia*, *S. planifolia* ssp. *tyrrellii*, *Betula papyrifera*, *Drosera rotundifolia*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Epilobium angustifolium*, and *Tanacetum huronense* var. *floccosum.*

In zone 6, where sand was infiltrating the dune slack, there were numerous young sporophytes of *Lycopodium inundatum*, seedlings of *Agrostis scabra, Juncus brevicaudatus, Salix brachycarpa* var. *psammophila*, *S. pyrifolia*, *S. planifolia* ssp. *tyrrellii*, *Betula glandulosa*, *Orthilia secunda*, and young gametophores of *Pogonatum.*

The dune invading this depression (zone 7) was covered by *Calamagrostis stricta* agg., *Carex aquatilis,* and *Tanacetum* which apparently were growing up through the dune. The large dune (zone 8) advancing toward the series of dunes and depressions supported only *Betula papyrifera* and *B.* × *sargentii* on its crest.

The complex dune and depression pattern that has just been described cannot be understood in terms of a simple vegetational succession pattern. Seedlings of almost all of the available species are able to grow in the wet or moist dune slacks, particularly in those parts of the slacks onto which sand is slowly infiltrating. Species typical of the

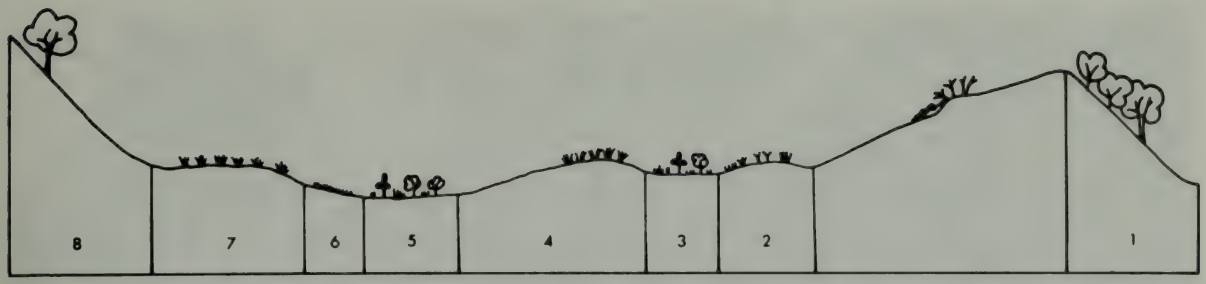


Figure 48. Profile of a buried drainageway just north of Ennuyeuse Lake. The sand is moving from left to right.

moving sand, in such genera as *Achillea*, *Tanacetum*, and the dune grasses, can also become established on shallow sand dunes. The dune slack habitat is localized and ephemeral, and it is subject to invasion by sand, which precludes the formation of a stable vegetation. Even when the dune slacks are large and have a vegetation that resembles that of stabilized sites, the active dunes surrounding them will eventually invade them and destroy the vegetation.

The Vegetation on Stabilized Aeolian Topography

There are two major forest types in the Athabasca sand dune region. Jack pine (*Pinus banksiana*) is the primary tree on the excessively drained sands and gravels of ancient beaches, stabilized dunes, sandy-gravel ridges, and sand plains. At the other end of the moisture gradient is wetland muskeg forest, primarily of black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Intermediates between these types, which might be called "mesophytic," are extremely variable and widespread, but they occupy, collectively, a relatively small fraction of the land surface. The two major habitats, dry and wet, are usually rather sharply defined. The boundaries between these habitats, however, are much blurred by the vegetation, which is higly variable, fragmentary, and difficult to define. Probably this is due to two main factors. One is the prevalence of forest fires, the incidence and effects of which are discussed elsewhere in this paper. The disturbing influence of fire is greatest, of course, in pine woods, but in very dry seasons wetland forests may also be burned. The second factor, and probably the more significant, is the wide moisture tolerance of the principal species. Usually, but not always, mixtures of jack pine, white and black spruce, and paper birch occur at sites where the water table is just below the surface or on small local flood plains along streams. White spruce is usually considered the most mesophytic tree in the region, but it also flourishes on the driest sand ridges. Black spruce is characteristic of wetland muskegs where jack pine and white spruce usually are not found. But it is also abundant on high sandstone bluffs near Poplar Point where it grows in cracks in the flat-lying rock. Jack pine grows on the driest sand hills and also thrives in low ground where the water table is very near the surface. Paper birch, though not abundant in the region, is found in mesophytic sites and also on active dunes.

Forests on Dry Sites

The most common forest type growing on stabilized dunes and on the sandy till plains south of Lake Athabasca is open jack pine-lichen forest (Figure 49). When young, these forests are dense but as the trees mature they become widely spaced and park-like, with very little upright shrub growth and with a ground cover of fruticose lichens, xerophytic mosses, a few scattered herbs, and occasional mats of trailing shrubs. In some places pine is the only vascular plant. In other places there are occasional white spruce or paper birch and one or two other species usually including *Hudsonia tomentosa*, *Empetrum nigrum*, *Arctostaphylos uva-ursi*, and *Vaccinium myrtilloides*. If only a small area is studied, such as one quarter of a hectar, the flora is deceptively meager, but collections in many such areas have yielded upwards of 60 kinds of vascular plants. The following list could doubtless be enlarged:

Equisetum arvense, Lycopodium annotinum, L. dendroideum, Juniperus communis, Picea glauca, P. mariana, Pinus banksiana, Agrostis scabra, Calamagrostis stricta agg. *Festuca rubra*

Figure 49. Jack pine-lichen forest on sand.

ssp. *richardsonii, F. saximontana, Oryzopsis pungens, Dicanthelium acuminatum, Poa glauca, Carex abdita, C. aenea, C. siccata, C. tonsa, Juncus arcticus* ssp. *littoralis, Maianthemum canadense, Cypripedium acaule, Populus balsamifera, P. tremuloides, Salix planifolia* ssp. *planifolia, S. scouleriana, Alnus crispa, Betula papyrifera, Comandra umbellata* ssp. *pallida, Geocaulon lividum. Drosera routundifolia, Saxifraga tricuspidata, Amelanchier alnifolia, Potentilla tridentata, Prunus pensylvanica, Rosa acicularis, Rubus idaeus* ssp. *sachalinensis, Sorbus scopulina, Empetrum nigrum, Hudsonia tomentosa, Lechea intermedia* var. *depauperata, Epilobium angustifolium, Aralia nudicaulis, Cornus canadensis, Arctostaphylos uva-ursi* var. *coactilis, Chimaphila umbellata* ssp. *occidentalis, Ledum groenlandicum, Vaccinium myrtilloides, V. vitis-idaea, Apocynum androsaemifolium, Melampyrum lineare, Linnaea borealis* ssp. *americana, Campanula rotundifolia, Artemisia borealis, Hieracium umbellatum, Solidago decumbens* var. *oreophila, S. nemoralis* var. *longipetiolata;* lichen mats commonly composed of *Cladina arbuscula, C. mitis, C. rangiferina, C. stellaris, Cladonia amaurocraea,* and *C. gracilis;* and the mosses *Polytrichum juniperinum* and *P. piliferum* which often form pure mats or are intermixed with lichens.

Pine forests burn repeatedly and some record of the burns in an area may be recorded in the existing stands of trees. Burns sometimes appear on aerial photographs as a "meadow-like" vegetation which may occur over large areas. One such area, studied in 1935, proved to be a nearly pure stand of small jack pine about 12 to 15 years old (0.5 m tall, 2 cm in diameter); single trees or small dense stands of trees about 40 years old (2-2.5 m tall, ca. 5 cm in diameter); and a third class of trees about 130 years old (ca. 8 m tall, 22 cm in diameter). The trees shown in (Figure 49) are in the oldest age class. From these data it was evident that a major fire went through the area about 1920. As usually happens, some trees sur-

vived as individuals or small stands. Trees of the 40-year age class appeared after a fire that occurred about 1895. The oldest trees date from about 1805, which was also probably a time of fire.

In all of the pine forests observed, very few trees, to judge by their diameters and probable growth rates, could have been much older than 130–150 years. From this we suggest that few areas along the south shore of Lake Athabasca have escaped being burned for much longer than 150 years, and that any one spot may have been burned over about 20 times in the last 3000 years, which is probably as long as forests have been in this area.

The jack pine is particularly prolific at seeding after a fire because its cones ordinarily remain closed for many years, but open when subjected to intense heat. Germination is almost immediate, leading to a dense cover of seedlings (Figure 6). Along the winter road to Cluff Lake, skirting the western edge of the sand dunes and heading south of Ennuyeuse Lake, the *Pinus banksiana* forest was extensively burned in about 1970. One burn had regenerated to three to five year old *Pinus* seedlings. The primary species in this vegetation were *Agrostis scabra*, *Hudsonia tomentosa*, and *Carex tonsa*, and *Pinus* seedlings. Associated with them was *Carex aenea*. Older, park-like stands commonly have an admixture of *Populus tremuloides*, *Betula papyrifera*, *Salix* spp., and *Vaccinium myrtilloides*. The ground cover in such jack pine stands is composed mainly of species of the fruticose lichens *Cladonia, Cladina, Cetraria,* and *Stereocaulon*.

Well into the open William River dune field there are occasional patches of *Pinus banksiana* forest, some perhaps one kilometer wide and harboring many shallow ponds (Figure 48). Some of these stands appear to have been undisturbed for a long time. The trees seem to be of all ages, from young seedlings to old decrepit trees. There are no remains of burned wood on the ground and no fire scars on the older trees. The ground surface is gently rolling and appears to be dune topography. It is mostly covered by a dense mat of the fruticose lichens characteristic of open pine forest and has an abundant growth of *Vaccinium myrtilloides*. Some sand dune grasses including *Bromus pumpellianus*, *Deschampsia mackenzieana*, and *Elymus mollis* occur in these forests. In the low spots are large numbers of muskeg shrubs and black spruces. It is not certain whether these forests are relics of old woodland missed by the advancing sand or whether they have developed on dunal topography that has been partially deflated.

An exception to the predominance of jack pine on dry sites is its replacement by Alberta white spruce (*Picea glauca* var. *albertiana*) in a few situations. A traveller moving along the south shore of Lake Athabasca could easily get the impression that the country is covered with white spruce, for it forms most of the forest visible from the lake (Figures 7 & 11). A short walk inland shows that the spruce is confined to a few ridges (sometimes to only one) immediately above the shore where blowouts are frequent. At the western margin of the small dune area just southeast of Wolverine Point, there is a zone of blowouts in which the partially stabilized areas are occupied by park-like Alberta white spruce stands. Subtending them to westward are the usual dry pine woods on stable sands. The blown-out tops of ridges in the country a few kilometers southeast of Wolverine Point also support white spruce on the western edges of diagonal blowouts. Where the sand is being moved actively, the open woods of old jack pine are being removed; here the trees becoming bush-like, with many twisted or dead branches. That the spruce is only a temporary resident is shown by the fact that the forest on the more completely stabilized ridges is almost invariably of jack pine. This is further supported by the occurrence of one decrepit old spruce in a stand of young pines on a stabilized ridge. Its occurrence around blowouts suggests that it may be able to stand more physical disturbance than jack pine.

Forests on Intermediate ("Mesophytic") Sites

Combinations of species from wetlands and from the driest sites occur in seemingly infinite variety in and around the dune fields. Low places in the pine forests on the stabilized dune surfaces, most of them probably relicts from dune slacks, retain some soil moisture through all or most of the summer. Here the woods have a rather thin shrub layer of species drawn from the muskegs or damp sandy shores including: *Ledum groenlandicum, Kalmia polifolia, Andromeda polifolia, Chamaedaphne calyculata*, and *Vaccinium uliginosum*. Herbs seen in such places are *Calamagrostis canadensis*, *Spiranthes romanzoffiana*, and *Lycopus uniflorus*. Black spruce (*Picea mariana*) may also occur here.

Vegetation located in an intervale between parallel bands of large, parabolic dunes just south

of Yakow Lake contains a mature, closed forest of *Picea mariana*, *Pinus banksiana*, and *Betula papyrifera*. Associated with these trees are *Goodyera repens*, *Alnus crispa*, *Geocaulon lividum*, *Empetrum nigrum*, *Arctostaphylos uva-ursi*, *Ledum groenlandicum*, and *Vaccinium vitis-idaea*.

A still more mesophytic phase of the pine forest is seen occasionally, usually at the bases of the steep slopes of stabilized dune slipfaces and on the lower slopes of the adjoining dunes. Here *Picea mariana* and *Betula papyrifera* are sometimes abundant and become primary species in the assemblage. Common upright shrubs are *Alnus crispa*, *Salix scouleriana*, *Viburnum edule*, and *Ledum groenlandicum*. *Empetrum nigrum*, *Arctostaphylos ura-ursi*, and *Vaccinium vitis-idaea* are common trailing shrubs. Occasional herbaceous species are *Lycopodium annotinum*, *L. sitchense*, *Goodyera repens*. *Lathyrus ochroleucus*, *Vicia americana*, *Cornus canadensis*, *Apocynum androsaemifolium*, and *Melampyrum lineare*.

Intermediate combinations are found also toward the dry end of the moisture gradient. Along the shores of Lake Athabasca and at the mouth of the MacFarlane River is a series of old, stabilized beach ridges parallel to the shoreline. On one of these ridges a forest of *Picea glauca* and *Pinus banksiana*, estimated to be 150 years old, was observed. It contains a flora relatively rich for the area, including some species that are usually restricted to the active sand dunes. The flora included: *Agrostis scabra*, *Bromus pumpellianus*, *Elymus mollis*, *Festuca rubra* ssp. *richardsonii*, *Festuca saximontana*, *Poa pratensis*, *Carex abdita*, *C. tonsa*, *Juncus arcticus* ssp. *littoralis*, *J. vaseyi*, *Salix planifolia* ssp. *planifolia*, *Betula glandulifera*, *B. neoalaskana*, *Stellaria arenicola*, *Arabis lyrata*, *Amelanchier alnifolia*, *Potentilla norvegica*, *P. tridentata*, *Prunus pensylvanica*, *Rosa acicularis*, *Rubus idaeus* ssp. *sachalinensis*, *Empetrum nigrum*, *Hudsonia tomentosa*, *Epilobium angustifolium*, *Pyrola elliptica*, *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*, *Artemisia borealis*, *Hieracium umbellatum*, and *Tanacetum huronense* var. *floccosum*.

Perhaps the most mesophytic forest we have seen in the dune region is that limited to small local flood plains along streams such as Ennuyense Creek and the William and MacFarlane Rivers (Figures 55 & 60). The Alberta spruce (*Picea glauca* var. *albertiana*) is the primary species, and individuals reach greater heights and diameters than elsewhere in the region. Alaska paper birch (*Betula neoalaskana*) is often associated with it as a primary species. Common shrubs are: *Alnus crispa*, *Sorbus scopulina*, *Rosa acicularis*, *Ledum groenlandicum*, *Vaccinium myrtilloides*, *V. uliginosum*, and *V. vitis-idaea*. It usually has a ground cover of woodland mosses, *Aulacomnium palustre* and *Ptilium crista-castrensis*, and scattered here and there the following herbs: *Lycopodium annotinum*, *L. complanatum*, *L. dendroideum*, *Cypripedium acaule*, *Goodyera repens*, *Geocaulon lividum*, *Epilobium angustifolium*, *Aralia nudicaulis*, *Cornus canadensis*, *Chimaphila umbellata* ssp. *occidentalis*, *Trientalis borealis*, and *Linnaea borealis* ssp. *americana*. Anyone familiar with the boreal American spruce forest will recognize elements that are widely distributed across the northern part of the continent. This forest, however, contains species of both eastern and western phases of the boreal forest: from the east, *Cypripedium acaule*, *Vaccinium myrtilloides*, and *Aralia nudicaulis*; from the west: *Betula neoalaskana*, *Sorbus scopulina*, *Chimaphila umbellata* ssp. *occidentalis*, and the western variety of *Picea glauca* var. *albertiana*.

At the center of Little Gull Lake an island covered by a closed mesophytic forest of *Picea mariana* has apparently escaped burning or other disturbance. It has reached a stage of development not observed elsewhere in the area. Only two species of vascular plants, *Ledum groenlandicum* and *Vaccinium vitis-idaea* are associated with the black spruce. These shrubs occur as scattered individuals in a deep carpet of mosses. Of the twelve species of mosses collected in the area the most common are *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Orthodicranum montanum*, *Dicranum polysetum*, and *Pohlia nutans*. The island is fringed with boulders which appear to relate it to the till-covered terrain to the south side of the lake more than to the stabilized sand dune covered landscape to the north.

Wetland Vegetation

Between Cree Lake and Lake Athabasca, on the long gentle slope of Athabasca Sandstone that is mantled by sandy glacial tills, are wide expanses of wetland interspersed with dry sandy deposits. The water table in this mantle is relatively high, held up by the sandstone or by permanently frozen subsoil. Drainage northward and northwestward is variously interrupted by aeolian topography and by elongated ridges with an east-west, north-

south, or northeast-southwest orientation. Undrained or poorly drained depressions in which the water table is at or near the surface have produced the wetland vegetation. Ponds and small lakes are frequent.

Our knowledge of the wetlands is confined to those we have seen in and around the Lake Athabasca dunes, supplemented by studies in other parts of the Mackenzie drainage basin. The region between the Lake Athabasca dunes and Cree Lake is botanically unexplored.

Efforts to standardize the description and nomenclature of wetland habitats and vegetation in the boreal forest regions of the world are legion. None has proved acceptable much beyond the limits of the locality or region for which it was conceived, and even there agreement has never been complete. Probably this is due to the extreme variation, in both time and space, exhibited by these vegetations and their habitats. With modern knowledge of ecotypic variation within species, and of the instability of physical habitats, standardization can hardly be expected. In this paper we shall not attempt to fit our descriptive units and analysis of wetland vegetation into units derived elsewhere and shall use the simplest possible conceptual frame-work on which to describe and analyze them.

The common name for most of the wetlands in northern Canada and Alaska is "muskeg," an Indian word for a mossy bog, particularly one with hummocks or tussocks on the surface. It is applicable to nearly all of the wetlands in the region with which we are dealing. Exceptions are on the sandy or stony shores of Lake Athabasca, on the shores of some shallow sandy ponds, and in damp to wet short-lived slacks among the active dunes. In these exceptions the moss substratum is lacking or nearly so.

Muskeg vegetation usually has three forms: forest, shrub, and grass-sedge meadow, all of which freely intergrade. They are most easily identified when seen at a distance as "zones" around the shores of lakes and ponds. As such they are purely physiognomic units, distinguished by the forms of their primary species. In shallow basins without standing water, the whole surface may be covered by any one of the three forms. If ponds or small lakes are present, a fourth, offshore zone of aquatic plants, may or may not be present.

The vegetation zones around the shores of lakes and ponds are commonly interpreted as developmental stages in a "succession" from open water to forest. If such a succession actually occurs it requires that the water levels remain fairly constant over long periods of time, with no major physical disturbance of the shores by fire or windblown sand or the opening of new drainage channels. In this region, where all of these factors are or have been active, the assumption of such an orderly succession appears gratuitous. It is fully as reasonable to assume that all of the species came into their zones at approximately the same time and survived in those segments of the moisture gradient most suitable to their requirements.

This is suggested by the vegetation of the dune slacks which, by definition, are more or less temporary. The moisture supply is determined by the extent of deflation with respect to the water table, and the time available is determined by the rate of dune movement. Under these circumstances, any one or any combination of the muskeg or sandy shore assemblages can be found in the dune slacks in each of which all or most of the primary species must have arrived at about the same time. Some biological succession may occur in the slacks but, if so, its vegetational results must be fragmentary and indeterminate.

Muskeg Forest. The primary trees in the muskeg forests are black spruce (*Picea mariana*) and tamarack (*Larix laricina*) (Figure 50) occurring together or separately. The hummocky moss ground cover is different combinations of *Calliergon stramineum*, *Dicranum polysetum*, *Helodium blandowii*, *Orthodicranum montanum*, *Pleurozium schreberi*, *Pohlia nutans*, *Ptilium crista-castrensis*, *Sphagnum magellanicum*, and *S. recurvum*. Shrub growth is extremely variable in density and species composition from place to place, most of it drawn from the following group of species: *Salix bebbiana*, *S. planifolia* ssp. *planifolia*, *Myrica gale*, *Alnus crispa*, *Ribes hudsonianum*, *R. triste*, *Rosa acicularis*, *Empetrum nigrum*, *Ledum groenlandicum*, *L. palustre* var. *decumbens*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Vaccinium myrtilloides*, *V. uliginosum*, *V. vitis-idaea*, *Oxycoccus quadripetalus*, and *Viburnum edule*. Herbaceous species include: *Lycopodium annotinum*, *L. selago*, *Equisetum fluviatile*, *E. sylvaticum*, *Calamagrostis canadensis*, *Carex chordorrhiza*, *C. pauciflora*, *C. trisperma*, *Calypso bulbosa*, *Spiranthes romanzoffiana*, *Geocaulon lividum*, *Drosera rotundifolia*, *Coptis trifolia*, *Potentilla palustris*, *Rubus chamaemorus*, *Epilobium ciliatum* ssp. *glandulosum*,

Figure 50. *Picea mariana* muskeg on the shores of Little Gull Lake. A muskeg shrub vegetation appears on the shore in the foreground.

E. leptophyllum, *Cornus canadensis*, *Orthilia secunda*, *Pyrola asarifolia*, *P. elliptica*, *P. virens*, *Lysimachia thyrsiflora*, *Trientalis borealis* ssp. *latifolia*, and *Menyanthes trifoliata*.

As in the dry pine woods flora this is a composite list. In any one locality only a few species may be found. Among the shrubs, *Empetrum* and the Ericaceae are most common. The most common herbs are *Equisetum*, *Lycopodium*, *Geocaulon*, *Cornus*, *Orthilia*, and *Pyrola*. The appearance of other kinds of trees in the wetland forest adds to the floristic variability. More mesophytic species such as *Betula papyrifera*, *Picea glauca*, *Populus balsamifera*, and even *Pinus banksiana*, are occasionally found with the black spruce and tamarack, suggesting the wide habitat versatility in most of the forest trees of the region.

Muskeg Shrub. The ground cover in muskeg shrub vegetation is a hummocky mat of mosses in which the primary vascular plants are upright or decumbent shrubs (Figure 50). The water table is near the surface, or above it in depressions among the moss hummocks. Species from the wet meadows commonly appear in these places. *Picea mariana*, *Larix laricina*, and *Betula papyrifera* appear as seedlings or small trees, individually or in scattered clumps, or "peninsulas" from neighboring muskeg forest. The shrubs that give this vegetation its form are: *Salix pedicellaris, Betula glandulosa*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, and *Vaccinium uliginosum*. Other vascular plants that occur in this vegetation are: *Scheuchzeria palustris* var. *americana*, *Triglochin maritimum*, *Carex aquatilis*, *C. limosa*, *C. rostrata*, *Eriophorum chamissonis*, *E. gracile*, *E. vaginatum* ssp. *spissum*, *Salix athabascensis*, *S. planifolia* ssp. *planifolia*, *S. pyrifolia*, *Myrica gale*, *Sarracenia purpurea*, *Drosera anglica*, *D. linearis*, *D. rotundifolia*, *Potentilla palustris, Kalmia polifolia*, and *Menyanthes trifoliata*. These plants grow commonly in hummocky mats of *Sphag-*

Figure 51. Muskeg grass-sedge meadow on the shores of Ennuyeuse Lake. A jack pine woods occupies the higher ground in the background.

num, often with small pools of water between the hummocks, with sedges, grasses, and other plants found more frequently in the muskeg meadows.

Our records, combined from many observations, show that the herbaceous flora of the shrub muskegs contains at least 46 kinds of plants, of which 16 were found only in the shrub vegetation. Overlapping habitat tolerances are suggested by the distribution of the remaining 30. Fourteen were found also in the muskeg forest, five were also in the muskeg meadows (see below), and 11 were found in all three of these vegetations.

Muskeg Grass-sedge Meadow. The moss and humus mat is thinner and less continuous, and there is more free water on the surface in muskeg grass-sedge meadow than in the shrub muskeg (Figure 51). Shrubs, if they occur, are scattered or reduced to a few trailing or decumbent species. The plants that give form to this type are rushes, grasses, and sedges, mainly the latter. The species content varies greatly from one meadow to the next, so that generalization becomes difficult or impossible; but the following species are often found in this habitat: *Equisetum fluviatile*, *Sparganium minimum*, *Scheuchzeria palustris* var. *americana*, *Triglochin maritimum*, *Calamagrostis canadensis*, *Carex aquatilis*, *C. brunnescens* ssp. *sphaerostachya*, *C. chordorrhiza*, *C. diandra*, *C. lasiocarpa* ssp. *americana*, *C. limosa*, *C. michauxiana*, *C. oligosperma*, *C. magellanica* ssp. *irrigua*, *C. rostrata*, *Eleocharis palustris*, *Eriophorum chamissonis*, *E. gracile*, *Rhynchospora alba*, *R. fusca*, *Scirpus hudsonianus*, *Calla palustris*, *Salix pedicellaris*, *Myrica gale*, *Betula glandulosa*, *Stellaria crassifolia*, *Drosera anglica*, *D. rotundifolia*, *Potentilla palustris*, *Epilobium leptophyllum*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Lysimachia thyrsiflora*, *Menyanthes trifoliata*, *Utricularia cornuta*, and *Galium trifidum*.

Grass-Sedge Meadow on Sand. This vegetation differs from the muskeg meadow in having little or no substratum of humus or moss (Figure 52). Its habitat is widespread, although it is highly localized and covers a relatively small total area. The composite vascular flora of the grass-sedge meadow on sand is one of the largest in the region, with approximately 80 species, no less than 17 of which were not seen in any other habitat. This

vegetation occurs at the margins of some lagoons near the shore of Lake Athabasca, on sandy shores or bars along streams and on the shores of inland ponds or small lakes that have sand bottoms. All of these sites are notable for seasonal or longer-term fluctuations in moisture supply, or for physical instability of the sand.

Primary species found at one place or another are: *Equisetum fluviatile*, *E. arvense*, *Sparganium minimum*, *Agrostis scabra*, *Calamagrostis canadensis*, *C. stricta* agg., *Eleocharis palustris*, *Carex aquatilis*, *C. lasiocarpa* ssp. *americana*, *C. oligosperma*, *C. rostrata*, *Juncus arcticus* ssp. *littoralis*, *J. brevicaudatus*, *J. filiformis*, and *Potentilla palustris*.

Occasional shrubs occur scattered as individuals or small groups and are derived from the floras of muskegs or stream banks: *Juniperus communis*, *Salix lasiandra*, *S. pedicellaris*, *S. planifolia* ssp. *planifolia*, *S. pyrifolia*, *Betula glandulosa*, *Myrica gale*, *Alnus crispa*, *A. incana* ssp. *tenuifolia*, *Ribes triste*, *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Kalmia polifolia*, *Andromeda polifolia*, *Vaccinium uliginosum*, and *Viburnum edule*.

Plants in this vegetation that are not found in any other habitat are: *Torreyochloa pallida* var. *fernaldii*, *Carex buxbaumii*, *Eleocharis acicularis*, *E. quinqueflora*, *Scirpus cyperinus* var. *brachypodus*, *S. microcarpus* var. *rubrotinctus*, *Juncus bufonius*, *Rumex mexicanus*, *Sagina nodosa* ssp. *borealis*, *Ramunculus hyperboreus*, *R. reptans*, *Rubus pubescens*, *Cicuta bulbifera*, *Artemisia borealis*, and *Solidago graminifolia* var. *major*.

Aquatic Vegetation. The Lake Athabasca sand dune region is relatively poor in aquatic vascular plants. The shallow waters off the shelving sandy beaches of Lake Athabasca seem to have no aquatics or very few of them. Bays protected from violent wave and ice action are essentially non-existent. We have collected 20 species thus far, from lagoons behind raised beaches along the main lake, from small inland ponds and lakes, and from a few sluggish streams. Twelve of them are strictly aquatic: *Isoetes muricata* var. *braunii*, *Sparganium angustifolium*, *S. fluctuans*, *Potamogeton alpinus* var. *tenuifolius*, *P. epihydrus* var. *ramosus*, *P. perfoliatus* ssp. *richardsonii*, *P. pusillus* var. *tenuissimus*, *Eleocharis palustris*, *Nuphar variegatum*, *Nymphaea tetragona*, *Myriophyllum spicatum* ssp. *exalbescens*, *M. verticellatum* var. *pectinatum*, *Utricularia vulgaris* ssp. *macrorhiza*, and *Lobelia dortmanna*. The remaining seven are also commonly found on wet sand or a peaty substratum in the wet meadows or shrub muskegs: *Sparganium minimum*, *Potamogeton gramineus*, *Polygonum amphibium* var. *stipulaceum*, *Callitriche verna*, *Hippuris vulgaris*, *Utricularia intermedia*, and *U. minor*.

Minor habitats. Three additional minor habitats should be mentioned here. Stony shores of Lake Athabasca have a small, though varied, flora drawn from the nearby sand beaches or from wetland habitats that subtend the shore in some places. They are somewhat more stable than the sand and have more shrub vegetation. The other two habitats are almost non-existent in the area with which we are dealing: sandstone ledges and crevices, and ruderal habitats. We have a few notes on ledges and crevices from east of Poplar Point where sandstone cliffs approach the south shore of the lake, but in the dune country only a few low ledges appear in the beds of streams. Occasional introduced ruderals have been collected around trapper's cabins on the south shore of the lake, but we have made no studies of these sites. The opening of a road from the vicinity of Ennuyeuse Creek to Cluff Lake will no doubt bring in more ruderals.

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Figure 52. Sedge meadow on sand. A precipitation ridge northeast of Little Gull Lake invading a meadow of *Carex michauxiana*, *C. lasiocarpa*, and *C. oligosperma*.

including: Robert W. Nero, David J. White, Thomas Kovacs, George Ledingham, and F.H. Edmunds.

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Appendix A. Sand Dune Fields and Parabolic Dunes south of Lake Athabasca

The Maybelle River Sand Dunes

In northeastern Alberta, just south of the western end of Lake Athabasca and about 55 km south southeast of Fort Chipewyan, lie the Maybelle River sand dunes (Figure 53). They are positioned about 6 km north of Barber Lake and 3 to 5 km west of Maybelle River. The dunes are located on a string of small lakes that are tributary to Maybelle River. These dunes, together with a smaller dune field west of the Richardson River (not visited by our parties), comprise the largest areas of active sand in northern Alberta. The Maybelle River dunes cover about 2800 ha and lie at an elevation of about 275 m.

The dune field consists of two parabolic dunes that have coalesced and moved to their present position from at least as far west as the Richardson River (about 10 km). The dune field has a northern and a southwestern arm. Transverse dunes run parallel to the long axis of the north arm and perpendicular to the long axis of the southwest arm. The field exposes an undulating gravel pavement overlying sand. Within the dune field is a series of ponds and wet dune slacks draining into a small lake lying outside of the dune field.

The precipitation ridges on the eastern and southern edges of the dune field have a steep lee slope which is invading forests and lakes. The windward side of the dune system consists of low sand hills that are being stabilized by forest. The border ridges, which are recognizable on the aerial photographs as light lines long after the area around them has been recolonized by plants, are low ridges gently sloping on both sides or often with a slightly steeper lee slope.

The parabolic dune system in the Maybelle River area is somewhat intermediate in development between the simple parabolic dunes such as occur in the Archibald Lake area and the open dune systems, such as those west of the William River. It is possible that the Maybelle River dunes could develop into an open, self-sustaining dune system similar to the large dune fields in Saskatchewan if they were exposed to strong northeasterly winds. This would reopen the western or windward edge of the parabolic dunes, thereby preventing the encroachment of the forest. In the past, however, the western edge of the dune system has not been kept open and forest has reinvaded the site as the parabolic dune migrated eastward. It is probable that as the dune system is slowed by the Maybelle River and remains in that position for a long time it will become completely stabilized.

The flora of the Maybelle River sand dunes is sufficiently different from that of the Saskatchewan dunes to suggest that they have not been connected with the Saskatchewan dunes since their origin. The absence of all but one of the endemics known from the Saskatchewan dunes and the relatively recent origin of the parabolic dune complex support the assumption that the floras of the Alberta and Saskatchewan sand dunes have been isolated for a long time.

The William River Sand Dunes

The largest dune field lying south of Lake Athabasca is in the William River area between Ennuyeuse Creek and the William River (Figure 54). The main dune field does not touch the lake shore but starts about 3–4 km south of the lake and extends inland about 15 km. The dune field is about 12 km wide, forming a roughly rectangular area oriented northwest-southeast. The area of the field is about 16 558 ha. The northern boundary of the field roughly parallels the 245 m contour, about 30.5 m above the present lake level, and the southernmost extent of the field is at about 275 m.

From the air the dune system appears to be an extensive plain on which sand has been built up into a series of high dunes. The sand spills eastward into the William River (Figure 55) and westward into Ennuyeuse Creek. These drainages seem to act as barriers to expansion of the field by carrying sand north into Lake Athabasca. The northern and southern edges of the dune system consist of parabolic dunes some of which are separated from the main dune field.

The major part of the western half of the dune system is a flat to rolling gravel pavement. The surface is covered with a gravel of relatively uniform size and boulders are uncommon. No distinct till deposits or source materials for the pavement veneer were found in the William River dune area to compare with that seen in the Thomson Bay dunes. Some gravel pavements, however, have coarse inclusions, including boulders, which may represent a glacial till deposit.

A field of about 40 prominent oblique ridge dunes (Figure 54), trending in a northwest to southeast direction, forms a band through the center one-third of the dune field. Some of these dunes rise as much as 35 m above the gravel-covered surface, but in the southeastern part of the

Figure 53. Vertical aerial photograph of the parabolic sand dune complex west of Maybelle River. Transverse dunes are visible on the parabolic dune itself and border ridges can be seen trailing from the tips of the parabolic dune. (Alberta Dept. Energy and Natural Res. photograph 5803A.)

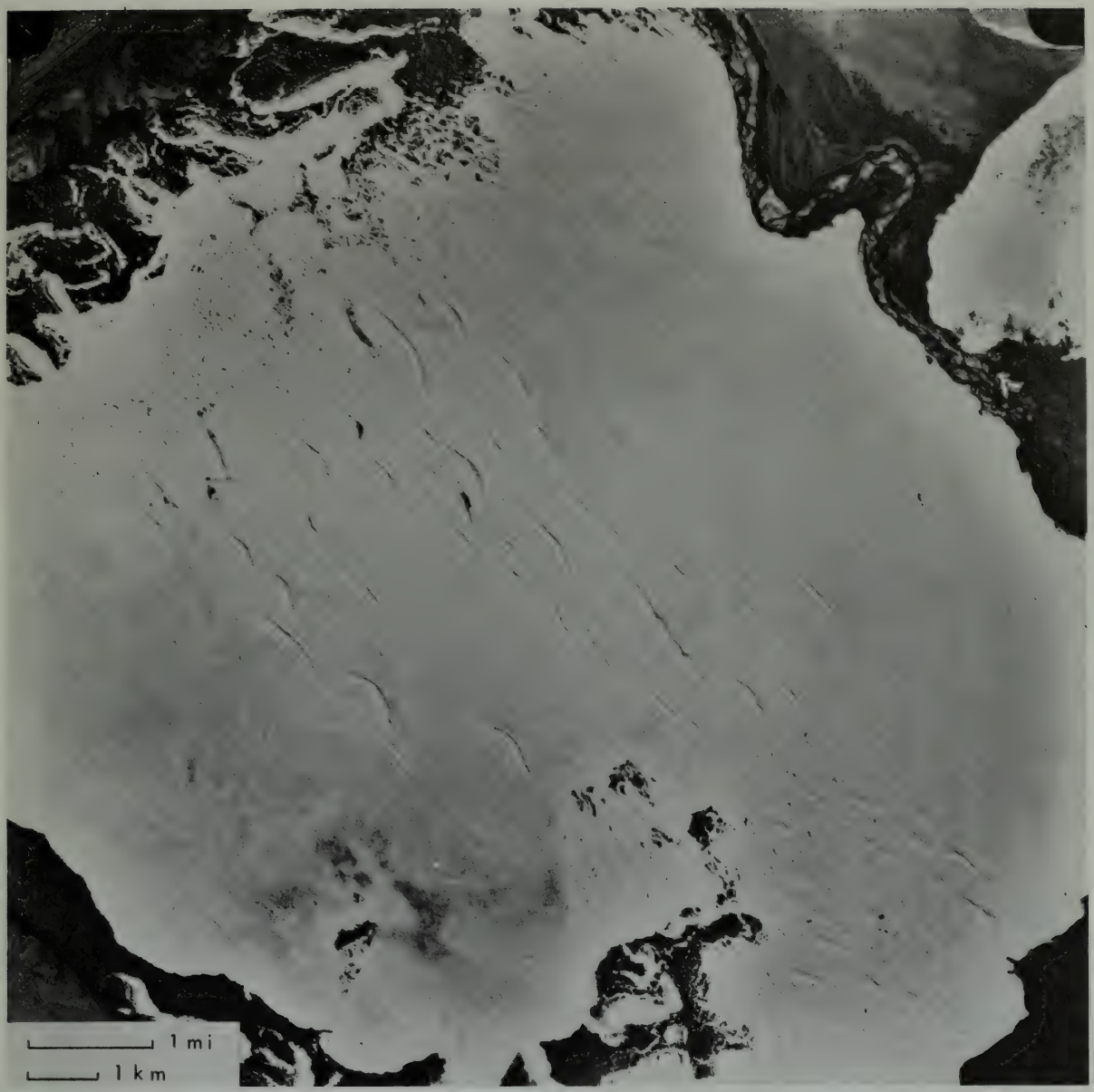

Figure 54. Vertical aerial photograph of the William River dune field. The William River traverses the upper right corner of the photograph and Ennuyeuse Creek traverses the lower corner. (National Air Photo Library photograph A-15611-9.)

field the dunes are low and indistinct. The large dune fields around the William River are influenced by both westerly and northeasterly winds that have a long fetch across many kilometers of open lake and across wide treeless sand fields. The precipitation ridges of these fields are well developed on all sides except on their northern and northwestern flanks. Under these circumstances, and over a long period of time, it might be expected that most of the available sand would be blown into the precipitation ridges. This does not appear to be the case, however, for the largest dunes in the William River field occur not in the precipitation ridges but in the middle of the field. In general, the dunes of the large fields, including the precipitation ridges, decrease in height and in volume the farther they are from the shore of Lake Athabasca.

Figure 55. Oblique aerial photograph of the William River looking north toward Lake Athabasca. The William River dune field appears on the left and a portion of the Thomson Bay field appears on the right. Floodplain forests of *Picea glauca* and *Betula neoalaskana* occur on islands in the foreground.

Figure 56. Oblique aerial view of the Lake Athabasca shore looking westward from Thomson Bay across the delta of the William River to Sandy Bay. A parabolic dune (center) moving southeasterly is meeting and overriding a precipitation ridge moving northwesterly from the Thomson Bay dune field.

The Thomson Bay Sand Dunes

Extending east of the William River about 16 km to Cantara Lake and from the shore of Lake Athabasca 8 km south to Little Gull Lake are the Thomson Bay sand dunes (Figure 56). This dune field covers about 9680 ha and lies between elevations of 214 m, at the lake shore, and 305 m inland. The eastern edge of the field grades into a complex of parabolic dunes which occur scattered, as isolated patches of sand, to the Wolverine Point dunes.

This large dune field, as well as the William River dune field, is best understood from the vantage point of Lake Athabasca for the lake has played a major role in its development. Along a transect from Lake Athabasca to Little Gull Lake the open dune area can be seen to rise in indistinct steps toward the south. The landscape near the shore consists of low transverse dunes or rolling dune topography usually covered by *Betula* or *Salix*. Farther inland the vegetation becomes sparser, consisting mainly of grasses and *Tanacetum*, and then all plants are absent near the center of the dune field. A little over half way into the dune field, gravel pavement appears and continues to a point near the southern edge of the field. In general, the dune area itself is featureless and monotonous consisting of low undulating dunes and gravel pavement ridges and plains. Near the southern edge of the dune field, the landscape is more complex with the appearance of wet dune slacks, precipitation ridges invading forests and muskegs, and with the development of parabolic dunes. The southern edge of the field parallels a drainage system including Little Gull Lake and a number of other smaller lakes. South of these lakes the landscape is a flat plain gradually rising southward. It is covered with gravel and a prominent elongated ridge which runs east-west just south of Little Gull Lake (Figure 6). This ridge is made up of an unsorted mixture of coarse stones and boulders in a sandy matrix. The plain on which the ridge is lying also consists of unsorted sand and gravel. There are no stabilized sand dunes in the area or other features that would suggest that this area was ever a part of an open dune field.

The importance of opposing winds in maintaining large open dune fields can be seen at the northwestern edge of the Thomson Bay dunes.

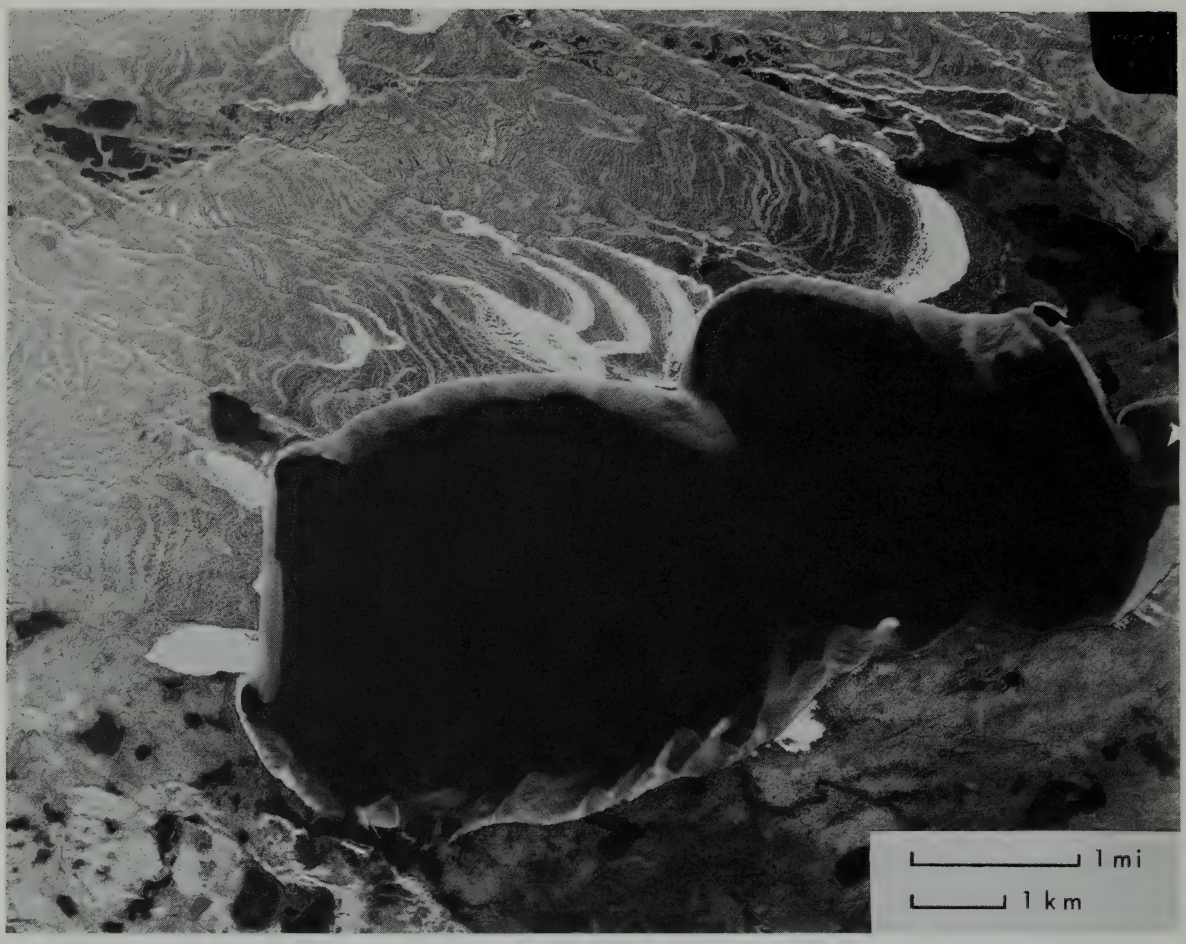

Figure 57. Vertical aerial photograph of Archibald Lake. A series of parabolic dunes meet the lake on its westerly and northerly shores. The tracks left by the dunes resemble an "embroidery" pattern. (Sask. Dept. of Tourism and Renewable Res. photograph H 14434-81.)

Here a parabolic dune, driven by northwesterly winds, is moving southeastward (Figure 56). Along its eastern edge the parabolic dune is invading and burying forest and along its western edge forest is reinvading the site.

The Thomson Bay dune field, itself, under the influence of opposing winds, is moving both northwestward as well as to the east and southeast and precipitation ridges occur along both its northeastern and northwestern edges. Where the parabolic dune and the dune field come into contact, the higher precipitation ridge of the parabolic dune is overriding the precipitation ridge of the dune field. It is probable that, as these two sand fronts merge the precipitation ridge will deflate slightly and will permit the easterly winds to reopen the western edge of the parabolic dune, thereby incorporating it into the larger dune system.

The Archibald Lake Sand Dunes

Located between the Thomson Bay dunes and those at Wolverine Point are the Archibald Lake dunes. The lake itself is located 13 km south of Turnor Point on the Lake Athabasca shore and 32 km east of William River. On the north shore of Archibald Lake there are six open parabolic sand dunes that have migrated from the west. The paths of the dunes are marked by stabilized dunes and border ridges (Figure 57).

On the north side of Archibald Lake there are alternating bands of low, stabilized sand dunes with intervening wet depressions. The active parabolic dunes in the area are moving across a stabilized, rolling sand plain and in places they are invading the lake. Four dunes are coalescing along the north shore of the lake and where they meet the lake a sand spit has been built. At the lake edge the old land surface is being eroded by the wind

Figure 58. Oblique aerial photograph of the easternmost of the three dune fields at Wolverine Point. (National Air Photo Library photograph A 2595-60.)

leaving perched remnants of forest. The largest of the active parabolic dunes is about 0.8 km long and 0.5 km wide and covers about 65 ha, but most of the dunes in the area are only half that size. These parabolic dunes are essentially large blow-outs with active dune fronts invading forest and wetland and having windward edges that are becoming stabilized by forest. The flora of these small, active sand dunes is much like that of the larger dune complexes and they include some, but not all, of the endemic taxa known from the major dune areas.

The Wolverine Point Sand Dunes

Three small dune fields lie on either side of Wolverine Point (Figure 1). The point is low, blunt, about 3 km wide at the base, and projects about 1 km into the lake. It is about 26 km west of the mouth of MacFarlane River. The Archibald River follows an eastward-bulging curve and then subtends Wolverine Point and enters Lake Athabasca at the western base of the point. There are low sandstone ledges in the bed of the stream a short distance above its mouth and some gravel in bars at the shore of the lake.

The two larger sand dune areas come out to the lake shore in shallow bays on either side of the point and a third smaller (probably parabolic) dune of about 40 ha is located on the point itself. The easternmost of the dune areas is about 1.5 km wide (N-S) and about 2 km long (E-W). It covers about 335 ha and lies between elevations of 214 and 245 m. The western dune area borders the west bank of the Archibald River for about 2 km above its mouth and then swings southward another 0.5 km making a roughly triangular mass about 1.5 km wide and reaching south from the lake about 3 km. It covers about 510 ha and lies between elevations of 214 and 275 m.

From the air (Figure 58), it can be seen that the eastern, southeastern, and parts of the southern margins of the Wolverine Point dunes are sharply defined against the dark gray tones of the forested surfaces. In contrast, the western and northwestern

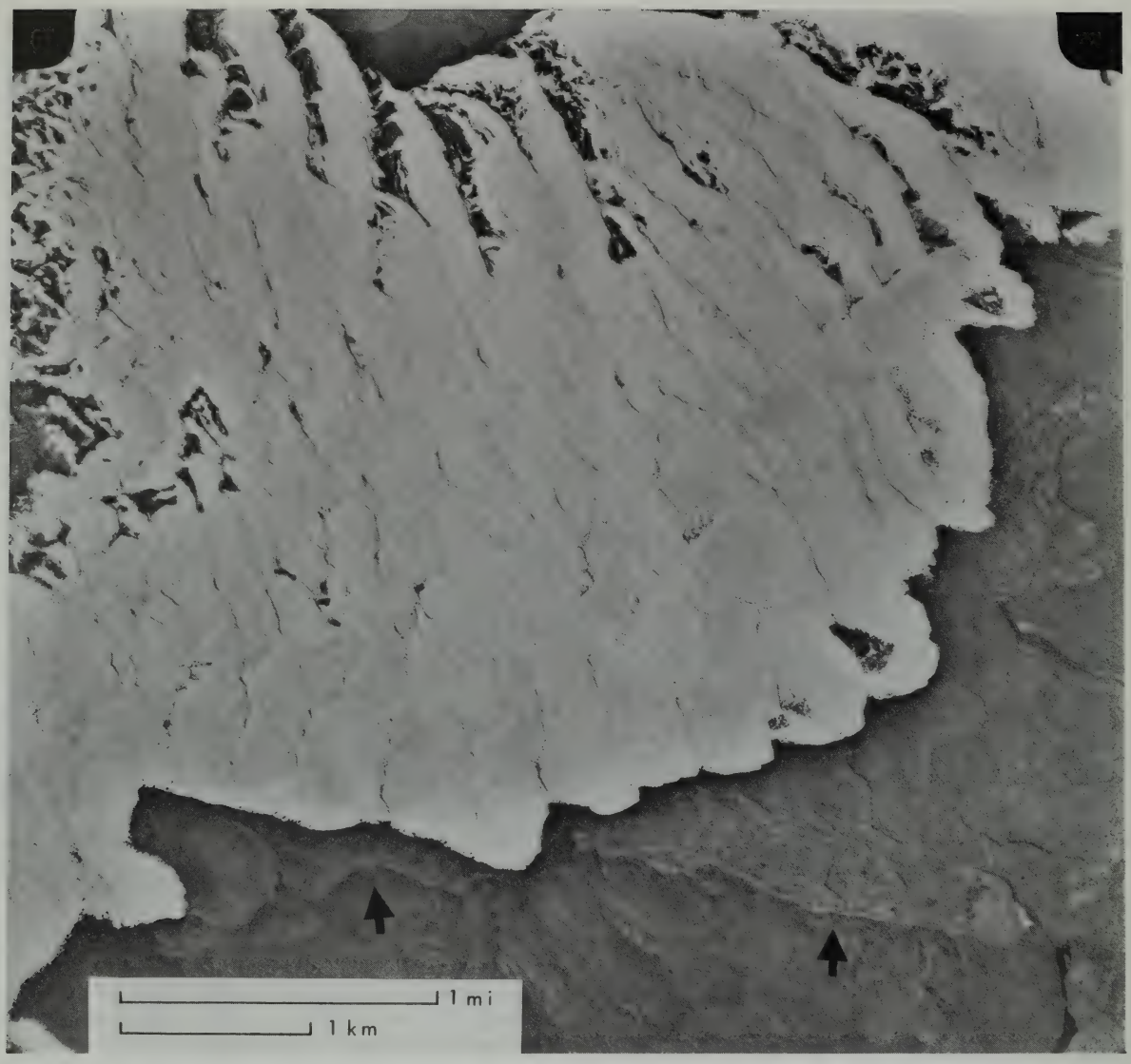

Figure 59. Vertical aerial photographs of the MacFarlane River dune field. Yakow Lake appears on the upper edge of the photograph and what appears to be an old precipitation ridge that has become stabilized by vegetation is indicated by arrows. (Sask. Dept. of Tourism and Renewable Res. photograph YC 7624-50.)

margins are "feathered out," showing a gradual transition from the sand to the forest, often with small areas of forest surrounded by open sand. At the eastern margin of the dunes a precipitation ridge, inundating a forest of *Pinus banksiana*, produces the sharply defined margins seen in the aerial photograph.

The western and northwestern margins are characterized by expanses of level or very gently rolling surfaces with trees widely spaced as individuals or small groves. The sand is partly stabilized by fruticose lichens, a few mosses, and trailing shrubs. West of these margins, the trees gradually become more frequent and the sand is more completely stabilized. Finally, a continuous forest with small sand blowouts appears.

It is probable that the amount of sand involved in the Wolverine Point dunes is not as great as would appear from surface observations. The gradually rising surface back of most of the lake shores is marked by high sand or gravel ridges that were formed on the receding shore of glacial Lake

McConnell and are counterparts of those that characterize the present shore. They and the smaller ridges and lagoon areas between them have supplied most of the sand for the dunes. The active dunes have completely effaced some of the ridges but others have maintained their identity as ridges or terraces among the dunes more or less parallel to the shore of the lake. These ridges may be composed of sand or gravel, depending on their position with respect to outcrops of sandstone or glacial till at the shores on which they were formed. Gravel pavements are common among the dunes where blowing sand has exposed them. On these areas ventifacts are often abundant.

The MacFarlane River Sand Dunes

A large dune field located near the eastern end of Lake Athabasca is bisected by the MacFarlane River. The main dune field, consisting of two more or less separated areas, extends about 10 km west of the river and a smaller dune area extends about 3 km east of the river (Figure 59). The western dune area touches Lake Athabasca at a point just west of Yakow Lake, its northern edge curves southeastward touching the south shore of Yakow Lake, and then swings eastward to the MacFarlane River meeting it at a point about 3 km from its mouth. The farthest inland extent of the main dune field is about 6 km south of Lake Athabasca and the smaller, eastern dune area lies about 5 km south of the lake. The western dune field covers about 4570 ha and the eastern dune area about 355 ha. The dunes lie between elevations of 214 m at the Lake Athabasca shore to 305 m at its inland limit.

The westernmost patch of open dunes almost reaches Lake Athabasca at its northern tip and it has well developed precipitation ridges on its eastern and southern flanks. The southern part of the western area is an extensive gravel pavement with scattered, shallow sand dunes moving across it. It is separated from the main dune field by a strip of vegetation about 5 km long and 1.5 km wide. There are signs of former extensive parabolic dune activity in this area but now it is almost completely covered by jack pine forest.

Along the northern edge of the main dune field there is a series of large parabolic dunes which have partially coalesced, leaving behind them parallel bands of forest running at right angles to the dune margin. The southern portion of the main dune field is a large area of sand plain and gravel pavement leading to precipitation ridges on its southern and eastern sides. In the central part of the main dunes there is a complex of intersecting sand dunes meeting each other at about right angles. The volume of sand in the MacFarlane River dunes seems to be less than that in the William River and Thomson Bay dunes and the water table is seldom exposed in the dune slacks.

The smaller dune area east of the river can be seen from the western dunes as sand cliffs along the shore (Figure 60). It appears to be spreading both to the east and to the west as indicated by the location of precipitation ridges.

Unvisited Saskatchewan Sand Dunes

Between Thomson Bay and Royal Lake is a series of parabolic dunes and small dune fields that cover about 1820 ha. These dunes were not visited by our parties. From aerial photographs they appear to be similar to the dune fields in the Wolverine Point area or the smaller parabolic dunes north of Archibald Lake.

Figure 60. View of the MacFarlane River and a dune field east of the river. Floodplain white spruce-birch forests appear in the center.

Appendix B. Checklist of the Flora of the South Shore of Lake Athabasca.

The checklist of the flora is based primarily on voucher specimens that we have examined, but some sight records and literature records are included as indicated. Major collections of voucher specimens of the vascular flora are housed in ALTA, CAN, DAO, GH, and SASK; the bryophytes in CANM, SASK, and UAC; and the lichens in CANL, COLO, SASK, UAC, and US (herbarium acronyms follow Holmgren & Keuken, 1974). Most of the collections were identified by the authors, but the following botanists aided in the identification or verification of certain groups: I.M. Brodo, H. Crum, A. Cronquist, M. Hale, V. Harms, R. Ireland, I.M. Lamb, J.W. Thomson, W. Weber, and P.Y. Wong.

Vascular Plants

LYCOPODIACEAE
Lycopodium annotinum L.
L. clavatum L.
L. complanatum L.
L. dendroideum Michx.
L. inundatum L.
L. selago L.
L. sitchense Rupr.
SELAGINELLACEAE
Selaginella rupestris (L.) Spring
ISOETACEAE
Isoetes muricata var. *braunii* (Engelm.) Reed
EQUISETACEAE
Equisetum arvense L.
E. fluviatile L.
E. palustre L.
E. sylvaticum L.
POLYPODIACEAE
Gymnocarpium dryopteris (L.) Newm.
Polypodium vulgare ssp. *virginianum* (L.) Hult.
CUPRESSACEAE
Juniperus communis L.
PINACEAE
Larix laricina (Du Roi) Koch
Picea glauca var. *albertiana* (S. Brown) Sarg.
P. mariana (Mill.) BSP
Pinus banksiana Lamb.
P. banksiana × *contorta* Loud.
TYPHACEAE
Typha latifolia L.
SPARGANIACEAE
Sparganium angustifolium Michx.
S. fluctuans (Morong) B.L. Robinson
S. minimum (Hartm.) Fries
NAIADACEAE
Potamogeton alpinus ssp. *tenuifolius* (Raf.) Hult.
P. alpinus var. *subellipticus* (Fern.) Ogden
Potamogeton epihydrus var. *ramosus* (Peck) House
P. gramineus L.
P. obtusifolius Mert. & Koch
P. perfoliatus ssp. *richardsonii* (Benn.) Hult.
P. pusillus var. *tenuissimus* Mert. & Koch
JUNCAGINACEAE
Triglochin maritimum L.
SCHEUCHZERIACEAE
Scheuchzeria palustris ssp. *americana* (Fern.) Hult.
ALISMATACEAE
Sagittaria cuneata Sheldon
POACEAE
Agropyron smithii Rydb.
A. trachycaulum (Link) Malte
Agrostis scabra Willd.
Bromus pumpellianus Scribn.
Calamagrostis canadensis (Michx.) Beauv.
C. lapponica (Wahlenb.) Hartm.
C. purpurascens R. Br.
C. stricta (Timm) Koeler agg. (incl. C. *stricta* ssp. *stricta* and ssp. *neglecta* (Gray) C.W. Greene)
Deschampsia mackenzieana Raup
Dichanthelium acuminatum (Swartz) Gould & Clark (*Panicum subvillosum* Ashe)
Elymus mollis Trin.
Festuca rubra L. ssp. *rubra*
F. rubra ssp. *richardsonii* (Hook.) Hult.
Festuca saximontana Rydb.
Glyceria borealis (Nash) Batchelder
G. pulchella (Nash) Schum.
Hordeum jubatum L.
Koeleria macrantha (Ledeb.) Schultes (*K. cristata* (L.) Pers.)
Oryzopsis pungens (Torr.) Hitchc.
Phragmites australis (Cav.) Steudel (*P. communis* Trin.)
Poa glauca Vahl
P. lanata Scribn. & Merrill
P. pratensis L.
Torreyochloa pallida var. *fernaldii* (Hitchc.) Dore
Trisetum spicatum ssp. *molle* (Michx.) Hult.
CYPERACEAE
Carex abdita Bickn.

C. aenea Fern.
C. aquatilis Wahlenb.
C. brunnescens ssp. *sphaerostachya* (Tuckerm.) Kalela
C. buxbaumii Wahlenb.
C. canescens L.
C. chordorrhiza L. f.
C. deflexa Hornem.
C. diandra Schrank
C. lasiocarpa ssp. *americana* (Fern.) Hult.
Carex leptalea Wahlenb.
C. limosa. L.
C. livida (Wahlenb.) Willd.
C. magellanica ssp. *irrigua* (Wahlenb.) Hult. (*C. paupercula* Michx.)
C. maritima Gunner
C. michauxiana Boeckl.
C. oligosperma Michx.
C. pauciflora Lightf.
C. pseudocyperus L.
C. rostrata With.
C. rufina Drej. (unconfirmed report)
C. siccata Dewey
C. stenophylla ssp. *eleocharis* (Bailey) Hult. (Unconfirmed report)
C. tenuiflora Wahlenb.
C. tonsa (Fern.) Bickn. (*C. umbellata* var. *tonsa* Fern.)
C. trisperma Dewey
Eleocharis acicularis (L.) R. & S.
E. palustris (L.) R. & S.
E. quinqueflora (Hartm.) Schwarz (*E. pauciflora* Link.)
Eriophorum branchyantherum Trautv. & Meyer
E. chamissonis Meyer
E. gracile Koch
E. polystachion L. (*E. angustifolium* Honck.)
E. tenellum Nutt.
E. vaginatum ssp. *spissum* (Fern.) Hult.
Rhynchospora alba (L.) Vahl
R. fusca (L.) Ait. f.
Scirpus caespitosus L.
S. cyperinus var. *brachypodus* (Fern.) Gilly (*S. atrocinctus* Fern.)
S. hudsonianus (Michx.) Fern.
S. microcarpus var. *rubrotinctus* (Fern.) M. E. Jones
S. subterminalis Torr.

ARACEAE

Calla palustris L.

JUNCACEAE

Juncus alpinus Vill.
J. arcticus ssp. *littoralis* (Engelm.) Hult. (*J. balticus* var. *littoralis* Engelm.)
J. brevicaudatus (Engelm.) Fern.
J. bufonius L. (incl. var. *halophilus* Buch. & Fern.)
J. filiformis L.
J. stygius ssp. *americanus* (Buch.) Hult.
J. vaseyi Engelm.

LILIACEAE

Maianthemum canadense var. *interius* Fern.
Smilacina trifolia (L.) Desf.

ORCHIDACEAE

Arethusa bulbosa L.
Calypso bulbosa (L.) Oakes
Cypripedium acaule Ait.
Goodyera repens (L.) R. Br.
Spiranthes romanzoffiana Cham.

SALICACEAE

Populus balsamifera L.
P. tremuloides Michx.
Salix arbusculoides Anderss.
S. athabascensis Raup
S. bebbiana Sarg.
S. brachycarpa Nutt. var. *psammophila* Raup
S. brachycarpa × *pyrifolia*
S. brachycarpa × *turnorii*
S. discolor Muhl.
S. lasiandra Benth.
S. lutea Nutt.
S. pedicellaris Pursh
S. pellita Anderss.
S. planifolia Pursh ssp. *planifolia*
S. planifolia ssp. *tyrrellii* (Raup) Argus
S. pyrifolia Anderss.
S. scouleriana Hook.
S. silicicola Raup
S. turnorii Raup

MYRICACEAE

Myrica gale L.

BETULACEAE

Alnus crispa (Ait.) Pursh
A. incana ssp. *tenuifolia* (Nutt.) Breitung
Betula glandulifera (Regel) Butler
B. glandulosa Michx.
B. neoalaskana Sarg.
B. occidentalis Hook.
B. papyrifera Marsh.
B. × *sargentii* Dugle (*glandulifera* × *glandulosa*)
B. × *utahensis* Britton (*occidentalis* × *papyrifera*)
B. × *winteri* Dugle (*neoalaskana* × *papyrifera*)

SANTALACEAE

Comandra umbellata ssp. *pallida* (DC.) Piehl
Geocaulon lividum (Richards.) Fern.

POLYGONACEAE

Polygonum achoreum Blake
P. amphibium var. *stipulaceum* (Coleman) Fern.
P. lapathifolium var. *salicifolium* Sibth.
Rumex mexicanus Meisn.
R. occidentalis Wats.

CHENOPODIACEAE

Chenopodium album L.
Corispermum hyssopifolium L.

CARYOPHYLLACEAE

Sagina nodosa ssp. *borealis* Crow
Silene acaulis L. f. *acaulis*
S. acaulis f. *athabascensis* Argus
Stellaria arenicola Raup
S. crassifolia Ehrh.
S. longifolia Muhl.
S. longipes Goldie

NYMPHAEACEAE

Nuphar variegatum Engelm.
Nymphaea tetragona Georgi

RANUNCULACEAE

Caltha palustris L.
Coptis trifolia (L.) Salisb. (*C. groenlandica* (Oeder)
Ranunculus aquatilis var. *capillaceus* (Thuill.) DC.
R. gmelini DC.
R. hyperboreus Rottb.
R. lapponicus L.
R. reptans L. (*R. flammula* var. *filiformis* (Michx.) Hook.)

CRUCIFERAE

Arabis arenicola (Richards.) Gelert
A. lyrata ssp. *kamchatica* (Fisch.) Hult.
Capsella bursa-pastoris (L.) Medic.

SARRACENIACEAE

Sarracenia purpurea L.

DROSERACEAE

Drosera anglica Huds.
D, linearis Goldie
D. rotundifolia L.

SAXIFRAGACEAE

Saxifraga tricuspidata Rottb.
Parnassia palustris ssp. *neogaea* (Fern.) Hult.

GROSSULARIACEAE

Ribes hudsonianum Richards.
R. triste Pall.

ROSACEAE

Amelanchier alnifolia Nutt.
Fragaria virginiana ssp. *glauca* (S. Wats.) Staudt
Potentilla norvegica L.
P. palustris (L.) Scop.
P. tridentata Soland.
Prunus pensylvanica L. f.
Rosa acicularis Lindl.
Rubus chamaemorus L.
R. idaeus ssp. *sachalinensis* (Levl.) Focke
R. pubescens Raf.
Sorbus scopulina Greene

FABACEAE

Lathyrus ochroleucus Hook.
Vicia americana Willd.

CALLITRICHACEAE

Callitriche verna L.

EMPETRACEAE

Empetrum nigrum L.

HYPERICACEAE

Hypericum majus (Gray) Britton

CISTACEAE

Hudsonia tomentosa Nutt.
Lechea intermedia var. *depauperata* Hodgdon

ONAGRACEAE

Epilobium angustifolium L.
E. ciliatum ssp. *glandulosum* (Lehm.) Hoch & Raven
E. leptophyllum Raf.
E. palustre L.

HALORAGIDACEAE

Myriophyllum spicatum ssp. *exalbescens* (Fern.) Hult.
M. verticillatum var. *pectinatum* Wallr.

HIPPURIDACEAE

Hippuris vulgaris L.

ARALIACEAE

Aralia nudicaulis L.

APIACEAE

Cicuta bulbifera L.
C. mackenzieana Raup

CORNACEAE

Cornus canadensis L.

PYROLACEAE

Chimaphila umbellata ssp. *occidentalis* (Rydb.) Hult.
Monotropa uniflora L.
Orthilia secunda (L.) House
Pyrola asarifolia Michx.
P. chlorantha Sw.
P. elliptica Nutt.
P. minor L.

ERICACEAE

Andromeda polifolia L.
Arctostaphylos uva-ursi var. *coactilis* Fern. & Macbr.
Chamaedaphne calyculata (L.) Moench
Kalmia polifolia Wang.
Ledum groenlandicum Oeder
L. palustre var. *decumbens* Ait.

Oxycoccus quadripetalus Gilib.
Vaccinium myrtilloides Michx.
V. uliginosum L.
V. vitis-idaea ssp. *minus* (Lodd.) Hult.

PRIMULACEAE

Lysimachia thrysiflora L.
Trientalis borealis ssp. *latifolia* (Hook.) Hult.

PLUMBAGINACEAE

Armeria maritima ssp. *interior* (Raup) Pors.

GENTIANACEAE

Menyanthes trifoliata L.

APOCYNACEAE

Apocynum androsaemifolium L.

LAMIACEAE

Lycopus uniflorus Michx.

SCROPHULARIACEAE

Melampyrum lineare Desr.
Pedicularis parviflora Smith
Rhinanthus crista-galli L.
Veronica americana Benth.

LENTIBULARIACEAE

Utricularia cornuta Michx.
U. intermedia Hayne
U. minor L.
U. vulgaris ssp. *macrorhiza* (LeConte) Clausen

RUBIACEAE

Galium trifidum L.

CAPRIFOLIACEAE

Linnaea borealis ssp. *americana* (Forbes) Hult.
Viburnum edule (Michx.) Raf.

CAMPANULACEAE

Campanula rotundifolia L.

LOBELIACEAE

Lobelia dortmanna L.

ASTERACEAE

Achillea lanulosa Nutt. ssp. *lanulosa*
A. lanulosa ssp. *megacephala* (Raup) Argus
Antennaria nitida Greene
Artemisia borealis Pall.
Aster puniceus L.
Erigeron acris var. *asteroides* (Andrz.) DC.
Hieracium umbellatum L.
Petasites palmatus (Ait.) Gray
Senecio congestus var. *palustris* (L.) Fern.
Solidago decumbens var. *oreophila* (Rydb.) Fern.
S. graminifolia var. *major* (Michx.) Fern.
S. nemoralis var. *longipetiolata* (Mack. & Bush) Palmer & Steyerm. (*S. nemoralis* var. *decemflora* (DC.) Fern.)
Tanacetum huronense var. *bifarium* Fern.
T. huronense var. *floccosum* Raup

Bryophytes

Andreaea rupestris Hedw.
Aulacomnium palustre (Hedw.) Schwaegr.
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.
Calliergon stramineum (Brid.) Kindb.
Ceratodon purpureus (Hedw.) Brid.
Dicranum polysetum Sw. (*D. rugosum* (Funck) Hoffm.)
Drepanocladus exannulatus (B.S.G.) Warnst.
D. uncinatus (Hedw.) Warnst.
Helodium blandowii (Web. & Mohr.) Warnst.
Hypnum lindbergii Mitt.
Orthodicranum montanum (Hedw.) Loeske (*Dicranum montanum* Hedw.)
Plagiomnium ciliare (C. Müll.) Kop. (*Mnium affine* var. *ciliare* C. Müll.)
P. ellipticum (Brid.) Kop. (*Mnium affine* var. *rugicum* (Laur.) B.S.G.)
Pleurozium schreberi (Brid.) Mitt.
Pogonatum urnigerum (Hedw.) P. Beauv.
Pohlia drummondii (C. Müll.) Andr.
P. nutans (Hedw.) Lindb.
Polytrichum commune Hedw. var. *commune*
P. commune var. *perigoniale* (Michx.) Hampe
P. juniperinum Hedw.
P. piliferum Hedw.
Pseudoleskella tectorum (Brid.) Broth. (*Leskea tectorum* (Funck) Lindb.)
Ptilium crista-castrensis (Hedw.) De Not.
Rhacomitrium canescens (Hedw.) Brid.
Sphagnum centrale C. Jens.
S. compactum DC.
S. majus (Russ.) C. Jens. (S. dusenii C. Jens.)
S. fuscum (Schimp.) Klinggr.
S. magellanicum Brid.
S. recurvum P. Beauv. var. *recurvum*
S. recurvum var. *brevifolium* (Lindb.) Warnst. (*S. recurvum* var. *mucronatum* (Russ.) Warnst.)
S. squarrosum Crome
S. teres (Schimp.) Angstr.
Sphagnum warnstorfii Russ.

Liverworts

Marchantia polymorpha L.
Ptilidium ciliare (L.) Hampe
P. pulcherrimum (G. Web.) Hampe

Lichens

Acarospora smaragdula (Wahlenb.) Mass.

Aspicilia cinerea (L.) Körb. (*Lecanora cinerea* (L.) Somm.)
Bryoria chalybeiformis (L.) Brodo & D. Hawksw.
B. furcellata (Fr.) Brodo & D. Hawksw.
B. fuscescens (Gyeln.) Brodo & D. Hawksw.
B. lanestris (Ach.) Brodo & D. Hawksw.
B. nadvornikiana (Gyeln.) Brodo & D. Hawksw.
B. simplicior (Vain.) Brodo & D. Hawksw.
Buellia lacteoidea B. de Lesd.
Cetraria cucullata (Bell.) Ach.
C. ericetorum ssp. *reticulata* (Räs.) Kärnef.
C. halei W. Culb. & C. Culb.
C. hepatizon (Ach.) Vain.
C. islandica (L.) Ach. ssp. islandica
C. laevigata Rass.
C. nigricans (Retz.) Nyl.
C. nivalis (L.) Ach.
C. pinastri (Scop.) S. Gray
C. subalpina Imsh.
Cetrelia olivetorum (Nyl.) W. Culb. & C. Culb.
Chaenothecopsis sp.
Chrysothrix chlorina (Ach.) Laundon, Ined. (*Lepraria chlorina* (Ach.) Sm.)
Cladina arbuscula (Wallr.) Rabenh. (*Cladonia sylvatica* (L.) Hoffm.)
C. mitis (Sandst.) Hale & W. Culb. (*Cladonia mitis* Sandst.)
C. rangiferina (L.) Nyl. (*Cladonia rangiferina* (L.) Wigg.)
C. stellaris (Opiz) Pouz. & Vězda (sight record)
Cladonia amaurocraea (Flörke) Schaer.
C. bellidiflora (Ach.) Schaer.
C. cenotea (Ach.) Schaer.
C. chlorophaea (Somm.) Spreng.
C. coccifera (L.) Willd.
C. cornuta (L.) Hoffm.
C. crispata (Ach.) Flot.
C. cristatella Tuck.
C. deformis (L.) Hoffm.
C. gracilis ssp. *turbinata* (Ach.) Ahti
C. phyllophora Hoffm.
C. sulphurina (Michx.) Fr.
C. uncialis (L.) Wigg.
Coelocaulon aculeatum (Schreb.) Gyeln. (*Cornicularia aculeata* (Schreb.) Ach.)
Dimelaena oreina (Ach.) Norm.
Evernia mesomorpha Nyl.
Huilia crustulata (Ach.) Hertel
Hypocenomyce scalaris (Ach.) Choisy (*Lecidea scalaris* Ach.)
Hypogymnia physodes (L.) Nyl. (*Parmelia physodes* (L.) Ach.)
Icmadophila ericetorum (L.) Zahlbr.
Lasallia pensylvanica (Hoffm.) Llano
Lecanora badia (Pers.) Ach.
L. chrysoleuca (Sm.) Ach. (*L. rubina* (Vill.) Ach.)
L. melanophthalma Ram.
L. polytropa (Ehrh.) Rabenh.
Lecidea auriculata Th. Fr.
L. epiiodiza Nyl. (*L. somphotera* (Vain.) Oliv.)
L. granulosa (Ehrh.) Ach.
Lecidella elaeochroma (Ach.) Haszl.
Lepraria sp.
Parmelia disjuncta Erichs.
P. exasperatula Nyl.
P. flaventior Stirt.
P. saxatilis (L.) Ach.
P. soredica Nyl. (*P. ulophyllodes* (Vain.) Sav.)
P. sorediosa Almb.
P. stygia (L.) Ach.
P. sulcata Tayl.
Parmeliopsis ambigua (Wulf.) Nyl.
P. hyperopta (Ach.) Arn.
Peltigera aphthosa (L.) Willd.
P. canina (L.) Willd.
P. malacea (Ach.) Funck
P. rufescens (Weis) Humb.
P. spuria (Ach.) DC.
Physcia adscendens (Th. Fr.) Oliv.
P. aipolia (Humb.) Fürnr.
Ramalina american Hale
R. dilacerata (Hoffm.) Vain. (*Fistulariella minuscula* (Nyl.) Bowler & Rundel)
R. intermedia (Nyl.) Nyl.
R. obtusata (Arn.) Bitt.
Rhizocarpon cinereovirens (Müll. Arg.) Vain.
R. geographicum (L.) DC.
R. grande (Flot.) Arn.
R. hochstetteri (Körb.) Vain.
R. norvegicum Räs.
R. reductum Th. Fr.
R. riparium Räs.
Rinodina sp.
Stereocaulon alpinum Laur. var. *alpinum*
S. alpinum var. *gracilentum* Magn.
S. botryosum Ach.
S. condensatum Hoffm.
S. glareosum (Sav.) Magn.
S. grande (Flot.) Arn.
S. paschale (L.) Hoffm.
S. rivulorum Magn.
S. tomentosum Fr.
Umbilicaria hyperborea (Ach.) Hoffm.
U. muhlenbergii (Ach.) Tuck.
Usnea cavernosa Tuck.
U. filipendula Stirt.

U. hirta (L.) Wigg.
U. sorediifera group
U. subfloridana Stirt.
Xanthoparmelia centrifuga (L.) Hale (*Parmelia centrifuga* (L.) Ach.)
X. conspersa (Ach.) Hale (*P. conspersa* Ach.)
X. incurva (Pers.) Hale (*P. incurva* (Pers.) Fr.)
X. separata (Th. Fr.) Hale (*P. separata* Th. Fr.)
X. taractica (Kremp.) Hale (*P. taractica* Kremp.)
Xanthoria polycarpa (Ehrh.) Oliv.

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